# Identification of stimuli and challenges to improve the environment of captive kea

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## Abstract

Inadequate environments can compromise the well-being of captive animals, at least in part because they may inhibit the expression of behavioural needs. There are several complementary approaches to assessing captive animal well-being, such as “function”, “feelings” and “natural-living” approaches. These rely on specific indicators (e.g. of physical health, fitness, physiology, suffering, expression of natural behaviours, motivation, and affective states) to assess if animals have poor or good well-being. To address the potential shortcomings of captive environments and improve captive animal well-being, additional stimuli, resources, or other behavioural engagement opportunities are often provided as environmental enrichment. Such “enrichment”, however, is commonly provided merely under the assumption that its well-being effects will be positive, with no prior evaluation. In addition, research on captive animal well-being can be biased towards certain enrichment types and certain taxa.

This thesis consists of a systematic investigation of stimuli, resources, and challenges to improve the environment of an understudied species of captive psittacine, the kea (*Nestor notabilis*), with a view to improving its well-being in captivity.

Kea are common across European zoos but research on their husbandry conditions and well-being is lacking. Information on other parrot species and on the behaviour of wild kea suggests that their well-being could be compromised in captivity. This thesis therefore starts with a survey of the husbandry and well-being of captive kea distributed to kea-keeping institutions. It finds that behaviours recognised as indicators of poor well-being in other captive psittacines (pacing, feather damaging, and abnormal reproduction) are also present in the kea population. It furthermore shows that enrichment practices have a bias towards foraging interventions.

This thesis then investigates a range of environmental stimuli and challenges identified as holding potential for improving captive kea well-being. This covers the effects of sensory stimulation on captive kea behaviour, of foraging interventions to promote foraging behaviours, and identifies preferred manipulations and challenges on the basis that animals have been shown to make choices that positively affect their well-being. Sensory stimulation is found to increase naturalistic behaviours and decrease behaviours associated with poor well-being and is thus interpreted as having a positive effect on kea well-being. Kea are found to contrafreeload, highlighting their motivation to perform a range of foraging strategies. Kea preferred to manipulate membranes when solving a foraging task and choose more often an arm of a T-maze containing a difficult visual discrimination task when an easy task was the alternative. These thesis findings may be used to shape improvements to captive kea well-being by designing motivating engagement opportunities that allow the expression of key behaviours.

## Dedication and acknowledgments

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Finally, thanks to my wonderful parents. The person I am know is all because of you. I dedicate this thesis to you as you also had to adapt to the changes of having me living abroad for all these years. This achievement is equally yours.

## Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED DATE

## Table of Contents

**Chapter 4. Evidence of contrafreeloading in a group of captive kea**



**Chapter 5. Effect of manipulanda and reward visibility on contrafreeloading**

**Chapter 6. Challenge preferences: do kea show a preference for levels of difficulty in a cognitive tasks?**

## List of Tables

## List of Figures

# Chapter 1. General Introduction

The general problem that this research project addressed relates to the provision of adequate captive environments for the study species, the kea parrot (*Nestor notabilis*) which could promote their well-being. The experiments here discussed belong to one of two general approaches. The first refers to the concept of environmental enrichment (see Section 1.5.2), in which specific resources (e.g. food, sensory stimuli, objects or tasks) are provided and evaluated in terms of behaviour-based well-being (see Sections 1.2.1 and 1.2.3). The second assumes that providing resources previously shown to be preferred by animals could enhance their well-being (see Section 1.2.2).

This chapter will discuss the background to this work. First, the concept of captive animal well-being[1] is defined. Next, an overview of the different approaches to measure well-being is provided, focusing on the "function", "feeling" and "natural-living" approaches. Then, the concepts of behavioural needs and behavioural deprivation are introduced as a framework to determine the behavioural requirements some species may have, which is further discussed in terms of foraging behaviour and contrafreeloading. Research on captive kea was found to focus on their performance in physical and cognitive tasks rather than on their well-being (see Section 1.4.2). Thus, the well-being and enrichment of other parrot species are reviewed to find opportunity areas and adequate methods. This chapter concludes with an overview of this project's aims and the general structure of the thesis.

## 1.1 Captive animals and their well-being

### 1.1.1 Past captive environments and early considerations towards animal needs

Animal captivity can be traced back between 16,000 and 12,000 years ago when prehistoric societies started keeping livestock to increase their numbers and utilise products or services derived from them (e.g. direct consumption, physical labour, clothing; Davis and Valla, 1978; Mazoyer and Roudart, 2006; Aland and Banhazi, 2013). The settings in which these animals were kept used to be very simplistic, with the natural environment providing the necessary barriers and shelters to create enclosures (Jarman, 1976) and satisfying basic animal needs (e.g. food and water).

Simmons and Dimbleby (1974) suggested that captive animal exploitation might have become more sophisticated during the Mesolithic (15,000–5,000 Before Present) as supplementary vegetation was provided to captive red deer during winter to ensure their

[1] Throughout this thesis, the term "well-being" is used synonymously to "welfare" (Mellor and Reid, 1994); but see Duncan (1993) for a semantic claim differentiating these terms based on "welfare" being used when describing feelings.

survival. During the Bronze Age (approximately 3,000 years BC), the keeping of livestock became more systematic with animals now housed in indoor, ventilated enclosures with hand feeding troughs and urine drains (Aland and Banhazi, 2013).

Besides the satisfaction of basic needs, there is indication that animal suffering was a problem that had to be prevented or remedied, evidenced by records dating back to the Bronze Age of healing experts, livestock treatments, and rabies control measures (Jones, 2011). This awareness of what animals required to thrive in captivity, and of their suffering, could be considered an early version or precursor of a concern for animal well-being.

### 1.1.2 Defining well-being

The definition of well-being seems to vary according to time and field. Early definitions by farmers and veterinarians focused on animals' "functions" and their living quarters (with a basis on natural science; Hewson, 2003). For example, in the 18$^{th}$ century, arguments were made to provide adequate stocking densities, avoid primitive enclosures, and ensure ventilation and access to daylight (Aland and Banhazi, 2013) as adequate captive conditions. As summarised by Hewson (2003): "if an animal is healthy and producing well, it is faring well". Good well-being was related to the biological functioning of organisms, which includes their growth, reproduction, health, and behaviour (Carenzi and Vega, 2009). Based on this approach, captive animals had good well-being when they can survive and reproduce (Barnett and Hemsworth, 1990).

In the 20$^{th}$ century, science began exploring the concepts of animal suffering and pain. Dawkins (1990) defined suffering as the result of subjective unpleasant feelings. Criteria relating to animals' physiological health such as diseases or injuries are "widely accepted as sources of suffering" (Dawkins, 1988) and of compromised well-being. Broom (1991a) further classified suffering as either fear (behaviours or experiences happening before or after a dangerous situation) or frustration (developing when animals possess knowledge on how to interact with their surroundings but are prevented to perform said interactions). The concepts of aversion (suffering caused by not being able to avoid a negative stimuli) and deprivation (suffering caused by the lack of stimuli that results in compromised behaviours) serve as an expansion for the definition of suffering (Dawkins, 1988). A further improvement to the definition of well-being includes the absence of suffering[2].

[2]There is a degree of subjectivity that complicates the process of defining animal well-being based on suffering. For example, it is possible that an injured or diseased animal (which could be assumed to be in pain and thus have a compromised well-being) does not suffer due to analgesics (either natural

The literature does not seem to converge into a single well-being definition. Fraser and colleagues (1997) compiled a set of eight quotations to show the discrepancy among well-being notions. These referred to a variety of concepts, including performance of full behavioural repertoires, animals' feelings, fitness, physiological functioning, or psychological processes (see Table 2 in Fraser et al., 1997).

The World Organisation for Animal Health (2013) succinctly defined well-being as "how an animal is coping with the conditions in which it lives". This "coping" occurs in a continuum (Mellor and Reid, 1994) ranging from poor to good well-being. This thesis agrees with a well-being definition including physical and psychological components. Animals with good well-being are physiologically healthy, do not suffer, show signs of positive mental states, and are able to behave in ways homologous to that of wild conspecifics, if applicable (e.g. non-domesticated species).

### 1.1.3 Rationale for well-being research

For the case of production animals, human health and animal well-being appear intricately linked. "The health of our food and our protection against disease and starvation are all heavily dependent on animal welfare, regardless of whether those animals are actually subjectively experiencing anything at all" (Dawkins and Bonney, 2008). Thus, ensuring farm animals have good well-being is in the best interest of humans but, what about wild animals' well-being?

Research into the well-being of captive wild animals originated, in part, from ethical and moral principles. There is an increasing recognition of animals as having intrinsic value. Being under human care requires "that the animals' nature and capabilities must be respected and that their interests must be taken into account" (Swart and Keulartz, 2011). Recently, the field of "compassionate conservation" has tried to merge ideas from conservation biology and animal welfare science to attend the ethical dimension of conservation (Fraser-Celin and Hovorka, 2019).

Furthermore, there appears to be a strong public interest in the well-being of captive animals. The book "Animal Machines" (Harrison, 1964) detailed the UK's intensive farming practices and the public's criticisms towards these made the government appoint a committee to investigate the well-being of farm animals. The "Brambell Report" was published by the committee, detailing the "freedoms" that farm animals should receive. The Farm Animal Welfare Committee was created to monitor farming practices and it formulated

or artificial) or lack of consciousness (Broom, 1991), thus contradicting a suffering-based well-being definition. This contradiction only arises if injuries per se are considered a well-being problem.

the five freedoms as: freedom from hunger and thirst; freedom from discomfort; freedom from pain, injury or disease; freedom to express normal behaviours; and freedom from fear and distress.

A more recent example occurred with “Blackfish”, a 2013 documentary detailing the death of an orca *(Orcinus orca*) trainer and the captive conditions of these cetaceans. The negative shift in the public’s opinions towards orca captivity had a noticeable impact in orca-keeping aquaria in the USA, ranging from artists no longer supporting them, holiday companies no longer promoting them, public attendance decreasing, and the end of theatrical orca shows and captive breeding as ways of satisfying the clamour for orca well-being (Zaveri, 2018). The scope of this thesis is not to present an ethical discussion on animal captivity and well-being, but the reader can refer to Lane-Petter, 1967; Fraser et al., 1997; Webster, 2001 for this discussion.

## 1.2 Well-being assessment: broad concepts

Defining animal well-being is not easy given the multiple aspects that can be considered (e.g. physical, physiological, emotional). Well-being is inherently subjective: just saying that an animal has good or bad well-being is not a scientific conclusion per se. To assess well-being in a scientifically-sound manner, relevant data should be collected and analysed. The well-being literature identifies three approaches to guide studies assessing well-being: function, feelings, and natural living (Duncan and Fraser, 1997).

### 1.2.1 Function approach

This approach focuses on captive animals’ biological state and fitness. Diseases, injuries, reproductive failure, stress, and performing abnormal behaviours are factors associated with poor well-being (Meehan and Mench, 2006). Broom (1991b) identified specific indicators as a reference for suffering (and thus compromised well-being) under the function approach.

#### 1.2.1.1 Physiology

Heart rate variation (HRV) is an accurate indicator of autonomic regulation of cardiac activity in captive animals associated with stress under varying housing and management conditions (see von Borell et al., 2007 for an in-depth review). For example, HRV of farm animals has been shown to significantly increase when housed in anxiety-inducing conditions (e.g. horses in Reid et al., 2017; cows in Irrgang et al., 2015).

Endocrine responses are also considered as well-being indicators. Stressful situations “result in an increase in the production of glucocorticoids (GCs) and/or catecholamine secretions” (see Möstl and Palme, 2002 for an in-depth review). GCs are among the first hormones secreted when facing a stressful situation, usually produced minutes after a stressful event (Palme, 2012) and they are useful to analyse the effect of stressors at both short and long terms. To measure short term effects, GCs can be measured directly from blood samples; to measure long term effects, GCs can be measured by their metabolites in either salivary or faecal samples (Broom, 1986; Palme, 2012).

GCs and HRV are only two examples of physiological well-being indicators. Others include: adrenal hormones (e.g. Todini, 2007), hematologic parameters (e.g. Manciocco et al., 2011), noradrenaline (e.g. Marchant-Forde et al., 2012), body weight (e.g. Schumann et al., 2014), body temperature (e.g. Miranda-de la Lama et al., 2018), enzyme levels (e.g. Chulayo and Muchenje, 2017), body posture (e.g. Tallet et al., 2016), bone marrow fat (e.g. Raglus et al., 2019), eye surface temperature (e.g. Esteves et al., 2019), immunity parameters (e.g. Lv et al., 2018), among others (see Broom and Johnson, 1993 for a more in-depth review of these).

#### 1.2.1.2 Behaviour

Under natural conditions animals modify their behaviour in response to changes in their internal and external environments (Toates,1986). Deviations in behavioural responses from those normally expected under non-stressful conditions might show an animal is not coping with an environmental challenge (Broom, 1991). Abnormal behaviours are described as indicators in the well-being literature, as they are sometimes performed in stress-associated situations (see Mason, 1991a).

Stereotypical behaviours (or stereotypies) are defined as behaviour patterns that are repetitive, invariant, and have no obvious goal or function (Mason 1991a). Besides appearing environmentally induced, stereotypies can also develop due to psychiatric conditions or certain drugs (Mason, 1990). Stereotypies are considered abnormal behaviours because they are “statistically rare”, non-functional or cause self-harm (these are not mutually exclusive; Mason, 1990).

Frustrating, stressful, or fear-inducing situations may lead to captive animals displaying stereotypies. For example, hens engaged in pacing behaviour when denied a suitable nesting site (e.g. Duncan, 1970). Similarly, pacing behaviour in captive carnivores was correlated with their natural range size, travel distances and hunting styles (Kroshko et al., 2016), suggesting a link with frustrated behaviours (e.g. hunting or patrolling). Japanese

quail (*Coturnix japonica*) showed elevated fear and pacing behaviours when exposed to stressful, aversive events (e.g. ventilators, delayed access to food, physical restraint, noise) but pacing decreased when given opportunities to isolate from stressors (Laurence et al., 2014). A study by Feenders and Bateson (2011) analysed the development of locomotor stereotypies (somersaulting, looping, falling, back-flipping) on wild-caught and captive-bred starlings (*Sturnus vulgaris*). Wild-caught birds performed more stereotypies, attributed to fear-related escape responses and lower activity levels.

Under-stimulating (i.e. barren) environments have also been associated with stereotypy performance. Indian leopards (*Panthera pardus*) displayed more stereotypies when kept off-exhibit (smaller enclosures with fewer structural features) than when kept on-exhibit (Mallapur and Chellam, 2002). Farmed mink (*Mustela vison*) kits kept in cages with less resting spaces and occupational items showed higher stereotypy rates than those kept in cages with more of these resources (Hansen et al., 2007). Cage size was not found to affect the performance of stereotypies, as both groups had alternate access to small or large cages, highlighting the relevance of environmental quality over enclosure size.

Stereotypies are discussed as signs of poor well-being due to the contexts under which they develop and the behaviours from which they appear to originate (Mason, 1991b). Recent discussions on stereotypies, however, distinguish certain scenarios under which the behaviour does not appear to be correlated with poor well-being, such as when they fully substitute a natural behaviour or when they have soothing effects (see Mason and Latham, 2004 and Section 1.2.4 of this Chapter).

Broom (1991) also recognised hypo- and hyperactivity in captive animals as well-being related behaviours based on human psychology (e.g. extreme inactivity being associated with psychiatric disorders). Pig behaviour seems to align with this proposal, as pigs have poor well-being when they become apathetic and ignore environmental stimuli (Broom, 1991). Regurgitation and reingestion of food are other abnormal behaviours that show compromised well-being (e.g. bonobos in Miller and Tobey, 2012). Lameness, “a debilitating condition in which the affected animal attempts to reduce the weight borne by a particular limb” (O’Callaghan et al., 2003), is considered a well-being indicator in cattle as it is associated with foot lesions (Murray et al., 1996) and pain (O’Callaghan et al., 2003).

#### 1.2.1.3 Injuries and diseases

Disease incidence can indicate how a captive environment can be detrimental for well-being. Injuries are considered a biological cost to animals and thus relevant for their well-being (Hemsworth et al., 2014).

For example, in the broiler chicken industry, chickens often suffer from dermatitis associated with poor conditions (e.g. use of poor-quality litter; Broom, 2006). In battery-housed hens, almost 30% were reported to have broken bones (Gregory and Wilkins, 1989), explained as a differential effect between hens housed in battery cages against those with more space to exercise, as fewer exercising opportunities lead to weaker bones (Knowles and Broom, 1990).

#### 1.2.1.4 Fitness

If mortality rates are higher in captive environment A than captive environment B, environment A is said to involve poor well-being (Broom, 1991). The same conclusion can be reached if reproductive success (e.g. reproduction and number of offspring) is hindered in any given environment (Broom, 1991). However, breeding output presents an inconsistency in terms of well-being assessment, as some animals are shown to successfully reproduce in environments associated with poor well-being (e.g. dos intensively bred in “puppy mills”, Burger, 2014). Section 1.6.1.3 provides a brief discussion and examples of how these parameters are interpreted as well-being indicators.

### 1.2.2 Feelings approach

The feelings-based approach focuses on animals’ subjective experiences, emphasising the reduction of pain/suffering and the increase of comfort/pleasure (Meehan and Mench, 2006). A review by Duncan and Dawkins (1983) suggested that well-being analyses should take animals’ feelings into account on the basis of the conclusions of the “Brambell Report” (Command Paper 2836, 1965; see Section 1.2.1) and an early well-being definition by Hughes (1976), stating that animals’ mental health should be considered.

The correlation between animals’ preferences and feelings has been discussed to be favoured by natural selection, as fitness in different environments should co-evolve with “escape or settling” responses elicited by them (Levins, 1968). Unfortunately, it is not possible to converse with animals and directly enquire on their feelings, but research has taken several approaches to circumvent this challenge. Animal preferences have been used as “indirect evidence” of their feelings by allowing animals to choose several aspects of their environments with the assumption that their actions, made in their best interest, are representative of their feelings (Duncan and Dawkins, 1983).

Early poultry research provides examples on how preference tests have been conducted and interpreted. Dawkins (1977) performed four experiments to determine what environmental characteristics battery-kept hens “liked” that she described as “a first step towards developing experimental methods to deal with the mental experiences of animals”.

In her first experiment, hens could roam in two setups: 1) a large pen, or 2) in one of two battery cages attached to said pen. Analyses of the time spent in each environment showed that hens did not prefer either option as they spent similar amounts of time in each. A second experiment was performed to control for the possibility that being allowed continuous access to both environments diluted preferences. Hens (half battery-housed and half run-housed) were given the choice of being in battery cages or in an outside run. Hens that were routinely housed in batteries were shown to prefer access to the outdoor run and hens that normally lived in outdoor runs preferred this environment over batteries. In the third experiment, hens were given the choice to enter battery cages with conspecifics or an outdoor run with no conspecifics, under the assumption that hens positively value the presence of conspecifics (e.g. Dawkins, 1976). Against her hypothesis, hens chose more often to be in outdoor runs with no conspecifics. Lastly, methods were changed by replacing conspecifics in the battery cage with food and no resource in the outdoor run. Out of the ten subjects, seven showed a (non-significant) preference towards the outdoor run. Overall, hens appeared to "like" outdoor runs. While these tests were not able to measure mental states, they are a steppingstone for reaching such conclusions. Similar experiments (e.g. Mason et al., 2001; Nicol et al., 2009; Reijwart et al., 2016, 2018) have determined which environmental characteristics are preferred or avoided by captive animals but still lack clear "feelings" evidence.

Using feelings as well-being indicators may be inadequate based on their subjectivity and their dependence on self-reflection[3], as feelings are: "ill-defined, impossible to measure directly, and difficult to measure indirectly" (Duncan, 2002). Recent approaches have identified concepts such as affective state and cognitive bias as potential tools to circumvent these problems.

Affective states refer to animals' elementary emotional states or feelings relying on different arousal levels (ranging from low to high) and valence (positive or negative; Russell and Barrett, 1999; see Figure 1.1). Cognitive bias refers to "measures of cognitive function […] used as proxy indicators of affective state" (Mendl et al., 2009). A prime example of the relationship between cognitive bias and affective state is provided by Harding and colleagues (2004). In their experiment, rats were trained to press a lever when they heard acoustic cue A associated with food delivery and to not press a lever when acoustic cue B signalled the delivery of white noise and no food. After training, half of the subjects were housed in depression-inducing environments (unpredictable housing) and half in environments where these symptoms were not displayed. After nine days, "ambiguous"

[3] "Only I can know how I feel" (Duncan, 2002).

acoustic cues C with intermediate tones to those of A and B were presented as in the training phase. Rats housed in depression-inducing environments “were slower to respond and tended to show fewer responses to” C like those corresponding to A. This study concluded that rats housed in unpredictable environments judged ambiguous cues as negative, suggesting a reduced expectation of positive events. This study provided evidence for the use of cognitive processes as indicators of affective states (see Mendl and Paul, 2004).

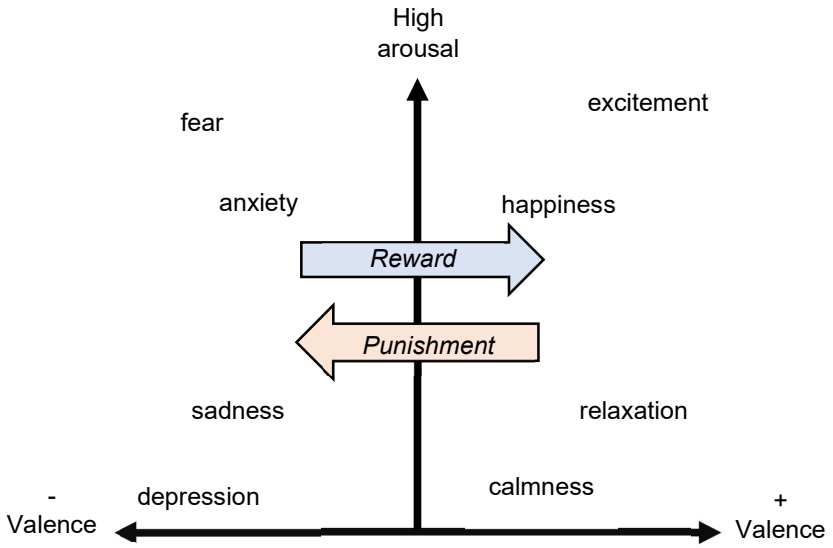



Figure 1.1 – Affective state spectrum with selected examples. Y axis represents arousal levels, ranging from high to low. X axis represents valence, ranging from positive to negative. Coloured arrows show examples through which affective states can shift in terms of valence (see Mendl and Paul for a detailed explanation). Adapted from Mendl et al., 2010.

### 1.2.3 Natural-living approach

The third well-being assessment approach derives from an ethical perspective. Fraser and colleagues (1997) introduced the concept of “natural living” to describe the conditions under which captive animals should be housed and their ability to live “naturally”. Initially, it was argued that since evolution favoured animals’ complete behavioural repertoires, they should be displayed in their entirety in captivity to promote their well-being (Kiley-Worthington, 1989). This framework was criticised as it assumed that behaviours displayed under stressful situations in the wild would show positive well-being if performed in captivity (Fraser et al., 1997).

Rollin (1993) introduced the concept of “telos” or “animals’ natures” to discuss how well-being research should focus on nurturing and fulfilling animals’ telos. Fraser and

colleagues (1997) reinterpreted the naturalistic approach by referring to animals' telos and discussing how captivity should allow animals to display their natural adaptations and undergo species-specific development. Under this approach, for example, "a pig in an indoor, straw-based pen system would be happier than a sow in a stall, but not as happy as a sow with free access to foraging and a shelter from inclement weather" (Rollin, 2007).

A problem of this approach relates to how "natural" is defined. From an anthropocentric perspective, "natural" could relate to a lack of human impact. Earlier assessments reported almost half of the world's terrestrial ecosystems to be disturbed by human impact (Hannah et al., 1993), complicating this anthropocentric approach. Melfi and Feistner (2002) supported a definition of "natural" in relation to species' wild environments, emphasising that these lie in a continuum ranging from wild to captive (Chang et al., 1999). However, comparing the behaviour of wild and captive animals involves certain caveats, such as more frequent human contact in captivity, temporal and geographic variation in wild behaviours, and lack of sufficient wild and/or captive data (Veasey and colleagues, 1996). Recently, a revision to the definition of natural behaviours was proposed by Bracke and Hopster (2006) as: "behavior that animals tend to perform under *natural* conditions, because it is *pleasurable* and promotes biological *functioning*." This revision highlights the interaction between the three well-being approaches.

The naturalistic approach has been broadly represented in zoo-based research, influenced by its ties to conservation and due to public opinions on how animals should be kept (Fàbregas et al., 2012). Rabin (2003) proposed the concept of "natural behaviour management" with the objective of "maintaining behavioural diversity in captivity and encourage behaviour […] in the presence of naturalistic stimuli". Under this approach, predatory and anti-predatory behaviours, for example, would be encouraged even if they involve stress, as these belong to species' natural repertoires.

Foraging behaviour is a recurrent example in the literature, as animals spend a substantial part of their activity budgets searching for food (Bracke and Hopster, 2006). In an experiment with semi-wild fowl (*Gallus gallus L.*), subjects were reported to spend 60% of their active time foraging even when food was supplemented by caretakers (Dawkins, 1989). Hens that could display foraging behaviours showed less cannibalism and feather pecking that hens that were not (Blokhuis, 1986), suggesting that the activity budget shift was replaced with behaviours associated with poor well-being. In another example, captive condors (*Vultur gryphus*) were fed small carcasses, which differs from their wild foraging habits. Gaengler and Clum (2015) analysed the delivery of large carcasses (closely resembling wild foraging habits), finding more physical engagement and longer foraging

durations; these results were interpreted as an improvement in their well-being. A similar study by Lindburg (1988) showed that captive felids (*Panthera tigris altaica* and *Acinony jubatus*) fed more naturalistically (carcasses instead of prepared foods) suffered less dental and oral problems, highlighting a connection between naturalistic and function-based well-being.

### 1.2.4 Is there an ideal approach to assessing well-being?

Techniques to measure well-being are directly influenced by the definition of well-being used as a framework (Mason and Mendl, 1993). If well-being is assumed to only include physical health (e.g. Broom, 1991), then the function-based approach appears relevant. On the other hand, animals in captivity as part of reintroduction programmes may be assessed under the naturalistic approach, as the expression of natural, species-specific behaviours would be necessary when reintroduced into the wild (Swaisgood, 2010).

Another issue occurs when indicators correlate with both positive and negative well-being. For example, male laboratory mice (*Mus musculus*) were housed in three different housing conditions: A) standard laboratory cages, B) standard laboratory cages with a box and scaffolding, and C) structurally-rich, spacious terraria (Marashi et al., 2003), expecting a positive well-being effect in conditions B and C based on behavioural and physiological parameters, as previous studies had shown that structural upgrades improved well-being (e.g. Broom and Johnson, 1993). Mice in conditions B and C were more aggressive and playful[4] than mice in housing A. This heightened aggression was expected because of new territories being defended but authors did not discuss this result in terms of well-being. Following the "natural-living" approach, aggressive mice were showing a natural behaviour, thus these environments positively affected their well-being. However, aggression may result in injuries which, under the "function" approach, would show poor well-being. Play behaviour has been discussed as a reliable indicator of good well-being as it correlates with relaxation and positive affective states (Broom and Johnson, 1993; Held and Spinka, 2011), thus mice in environments B and C showed improved well-being. Mice in environments B and C showed higher corticosterone concentrations, therefore, under the assumption that high corticosterone are associated with poor well-being (von Holst, 1998) and the function approach, housing B and C had a negative effect. Marashi and colleagues attributed

[4] Pay behaviour has been defined as those behavioral sequences differing from regular behaviours by being exaggerated, repetitive or incomplete (Smith, 1982). A recent revision of the definition adds these characteristics: not fully functional, self-rewarding, and displayed in a "relaxed field" (Burghardt, 2005). As play behaviour is displayed by wild animals (i.e. natural behaviour) and has been linked with positive emotions (Fraser and Duncan, 1998) it appears to be a convergence point of the feelings and natural-living well-being approaches.

corticosterone levels to aggressive behaviour and also noted that while corticosterone increased in environments A and B, these levels "were still within the normal range of nonstressed male mice" citing Dürschlag, 1999 (a PhD thesis) but no peer-reviewed literature.

This discussion on Marashi et al. (2003) is meant to stress how restricting well-being assessments to a single parameter may not be correct, as different parameters appear to correlate with well-being in different directions. Mason and Mendl (1993) provided an in-depth discussion on how different well-being measures appear contradicting, highlighting type of stimulus, animals' baseline psychological states, species, sex, and age as some "factors underlying the problems of welfare measurement". As discussed by Mendl (2001), there appears to be agreement that the different well-being approaches complement each other (e.g. Duncan and Fraser, 1997; Broom and Johnson, 1993; Dawkins, 1990). This thesis therefore supports a holistic well-being definition in which the three approaches should be followed, when possible, to provide an educated and correct assessment rather than relying on a single approach (or indicator).

### 1.3 Well-being triage: are some species more vulnerable to captivity than others?

Mason (2010) proposed a framework that uses the wild ecology and behaviour of species to predict how well they should adapt to captive environments considering a species-based comparative approach to determine traits linked with well-being. Her rationale was centred around four studies, discussed next.

Chamove et al. (1988) found that from twelve primate species, those with smaller bodies were most affected by zoo visitors (measured by reduced activity levels). Mettke (1995) compared exploration behaviour of six parrot species and determined that species prone to display feather damaging behaviour performed more exploration (measured by exploration of novel objects). Clubb and Mason (2003) analysed data on captive infant mortality and abnormal locomotor behaviours of 31 carnivore species, finding that "being naturally wide-ranging" predicted higher infant mortality and abnormal locomotion. Müller and colleagues (2010) compared the mean captive lifespan – maximum lifespan ratio of 20 deer species, finding that the percentage of browse in their natural diet negatively co-varied with the ratio.

Following this comparative approach, Mason (2010) reviewed the literature on animals' responses to "anthropogenic environmental changes in the wild" as a parallel to the

challenges that animals face in captivity and identified three key variables that could predict good well-being.

### 1.3.1 Boldness

A species is considered bold when it does not show fear responses to threatening situations (Stankowich and Blumstein, 2005). Being bold is considered beneficial in the wild, since fitness is less likely to be compromised (e.g. foraging interruptions due to freeze or flight responses or reproductive stress; Mason, 2010). Animals are described as adapted to captivity when their flight/escape propensity is reduced and they show a willingness to take enough food while ignoring stressors (Hediger, 1950). Mason (2010) referred to penguin species that are fearful towards humans and those that are not; fearful species showed reduced reproductive output in captivity, which was not the case for bold species. Under the assumption that captive environments present fear-inducing stimuli, bold animals should be more resilient to said stimuli and, therefore, their well-being should not be compromised.

### 1.3.2 Migratory patterns

Species whose wild ecology involves migratory movements are suggested to have poorer well-being in captivity than non-migratory species (Mason, 2010). Mason supported this hypothesis by discussing the work of Cassey and colleagues (2004), who analysed 350 parrot species to determine which variables influenced their successful transportation, release, and establishment. Data showed that, once released, migratory species were less likely to establish than non-migratory species. Mason interpreted this result with a comparison against invasive species (defined as “non-native species that threaten ecosystems, habitats or other species”, Convention on Biological Diversity, 2008). She described invasive species as thriving in novel environments and in proximity with humans, thus suggesting a parallel with captivity. Mason (2010) predicted that non-migratory parrot species would fare better in captivity.

Research on the white-crowned sparrow (*Zonotrichia leucophrys gambelli,* Landys et al., 2004), a migratory bird, appears to confirm Mason’s prediction. Sparrows were assigned to one of two groups: long photoperiods (associated with the time of the year during which they migrate) or short photoperiods. Birds in the long photoperiod treatment showed higher restlessness indicators such as increased corticosterone levels, supporting the hypothesis that constraining migratory behaviour negatively affects well-being.

### 1.3.3 Behaviour flexibility

Behavioural flexibility or plasticity is “the ability to cope with new stimuli or resources” and “involves being exploratory rather than avoiding novelty and being able to modify foraging and other behaviours to exploit new opportunities” (Mason, 2010). Behavioural flexibility is assumed to facilitate adaptation to captive settings. Animals with high behavioural flexibility are predicted to be less averse towards novel situations, as these should not pose a risk to their survival (Sol et al., 2013) when compared to animals with low behavioural flexibility. By being able to adapt behavioural responses, animals can: “find new food opportunities, use hard-to-extract foods, deal […] with unfamiliar enemies or change the way they communicate with conspecifics” (Sol, 2003).

Behavioural flexibility has been discussed as an explanation to why some animals cope better with situations such as human-induced rapid environmental changes (e.g. urbanisation in Sol et al., 2013) and captivity (Mason et al., 2013). For example, captive ruminants that prioritised certain types of vegetation were more likely to die than those with a general, grass-based diet (Müller et al., 2011). Research on zoo-housed carnivores indicated that species with “particular” (i.e. non-flexible) lifestyles[5] did not adapt well to captivity based on the expression of abnormal behaviours and higher rates of infant mortality (Clubb and Mason, 2003).

While Mason (2010) concluded that “behavioural inflexibility could well confer poor ability to habituate to human proximity or to suppress natural activities that captivity renders impossible or redundant”, Mason and colleagues (2013) appeared to refute this by stating “whether behavioural plasticity is a straightforward protective factor for species placed in captivity is unknown but unlikely. It seems doubtful that behavioural plasticity is always beneficial.” Mason et al. (2013) argued that behavioural flexibility is most beneficial in situations of “human-induced rapid environmental change” such as deforestation, urbanisation, climate change, and changes in predator or prey populations rather than in captive scenarios. Their reason for this differentiation was that captivity limits available space, environmental (physical) complexity and resource predictability, which in turn restrict learning opportunities and minimise the need to learn (or to be behaviourally flexible). However, following this rationale, if captive environments were to provide opportunities that promote learning and the expression of behavioural repertoires, then behaviourally flexible species should fare better. Baxter’s (1983) view of how animals’ environmental requirements

[5] Animal lifestyles included the following variables: home-range size, daily travel distance, time spent in general activity, time spent foraging, and reliance on hunting. See Clubb and Mason, 2003).

may be fully met in captivity if attention is placed on proper (environmental) design supports this assumption.

The relevant question then becomes: what makes captive environments adequate? The next section discusses the concept of **behavioural needs** as a descriptor for behaviours that animals need to express, and that captive environments should cater for.

### 1.3.4 Behavioural needs

Dawkins (1983) recognised that studies often examined behavioural needs without defining them. Legislation codes have already referred to behavioural needs, for example: by saying that not only physiological (e.g. food and water) but also ethological needs should be catered for in captivity (European Convention for the Protection of Animals kept for Farming Purposes); by referring to basic needs such as the opportunity to display normal behaviour patterns (MAFF, 1983); and by commenting on how captivity may disturb animals' behavioural urges (Brambell Report, Command Paper 2836, 1965). While not providing a definition, these explanations suggested that animal well-being would be compromised if behavioural needs are not satisfied.

Dawkins (1983) presented a framework based on ultimate and proximate needs to construct a definition for behavioural needs. Ultimate needs are those which, if not met, result in either death or reproductive failure (Baker, 1938). Nest-building, foraging, and predator-avoidance are examples of ultimate needs. Proximate needs are those that, if not met, do not result in death or impaired reproduction. Dawkins (1983) mentioned the example of battery hens and dustbathing. Hens appear motivated to dustbathe as they sometimes perform this behaviour in a non-functional context (e.g. bathing on bare wire floors), which is interpreted as hens having an intrinsic drive to bathe (e.g. Hughes, 1980).

Kornum and colleagues (2017) summarised the literature on behavioural needs and listed the following characteristics to determine which behaviours should be considered needs:

- Behaviours that are performed by all members of a single species,
- Behaviours whose deprivation results in stress,
- Behaviours caused by intrinsic rather than extrinsic (i.e. environmental) parameters,
- Behaviours whose deprivation results in an accumulation of motivation or drive to be performed,
- Behaviours that are self-rewarding.

Jensen and Toates (1993), however, disagreed with the notion of behavioural needs. They discussed how behaviours that are assumed to be “needs” do not cover the characteristics mentioned above. For example, sows in the farming industry have been reported to build nests before giving birth whilst free-ranging, and this behaviour has been classified as a need given that it: results in reproductive success, appears triggered by internal factors (e.g. physiology, Lawrence et al., 1994) and is performed by captive sows across all housing conditions (Jensen et al., 1993). It could be hypothesised that tethered or confined sows, able to perform the physical movements necessary for nest-building even in the absence of nesting materials, should not have a compromised well-being (Jensen, 2001). However, confined sows show higher cortisol levels when compared to non-confined sows with access to straw (Lawrence et al., 1994) thus suggesting poor well-being. An explanation for this effect refers to confined sows with no nesting material lacking behaviour-based feedback; contrarily, free-ranging sows are able to adapt and modify their nest-building behaviour based on environmental conditions (Jensen, 1989; Jensen, 2001).

Jensen and Toates (1993) commented on the distinction between needs and “non-needs”, arguing that the full, natural behavioural repertoire of an animal should be considered, rather than focusing on identifying which specific behaviours are “needs”. They recognised that not being able to display species-specific behaviours in captivity often leads to suffering.

### 1.3.5 Behavioural deprivation

Behavioural deprivation occurs when a captive animal is not able to perform a behaviour due to environmental restrictions (Dawkins, 1988). Early research discussed that when captive animals are prevented from displaying behaviours that occur in the wild (or when free-ranging), there is a negative effect on their well-being based on suffering (Martin, 1975; Farm Animal Welfare Council, 1986; Koene, 2013).

Following a similar approach to Millar (2013), the following discussion on behavioural deprivation uses foraging behaviour as an example of how captivity may compromise it given its evident association with fitness and its predominance in the literature. The reader should not interpret this decision as attributing more importance to this behaviour. As signalled by Millar (2003), food is often provided to captive animals in simplistic ways (e.g. in a free-to-access bowl) “reducing their foraging duration to a few minutes” and preventing the display of foraging-related behaviours. Other characteristics inherent to captive environments, such as enclosure size, also appear to affect the foraging response.

For example, female pigs developed abnormal behaviours (i.e. behaviours absent in free-ranging pigs) due to foraging restrictions in captivity (Lawrence and Terlouw, 1993). The behaviour of free-ranging pigs is characterised by “rooting and nosing at the ground”, disturbing it to obtain food items (Mason and Mendl, 1997). In farms, sows are commonly kept in solid-floored pens for better management with foraging behaviour restricted to food containers. Sows have been shown to perform redirected, non-functional foraging behaviours (e.g. towards elements such as chains and bars, Jensen 1988, Terlouw et al., 1991). The provision of straw to mimic the natural environment and to allow the expression of foraging behaviour has been shown to reduce the performance of abnormal behaviours (Spoolder et al., 1995).

The keeping of felids in zoos also appears to constrain foraging behaviours as they are commonly fed in simplistic ways that restrict behaviours common in the wild such as searching, hunting, or pursuing. Shepherdson and colleagues (1993) changed the feeding protocol of captive felids to determine behavioural changes. Baseline conditions consisted of food being presented once per day in a bowl on the floor. One fishing cat (*Felis viverrina*) was given the opportunity to hunt live fish placed in enclosure pools (in addition to baseline feeding) and four leopard cats (*Felis bengalensis*) received multiple feedings per day instead of baseline conditions. Initially, food was still placed on the floor but in a second phase, food was hidden in brush piles. Data showed that subjects’ behaviour changed by engaging in behaviours displayed in the wild (fishing and searching for food) which resulted in an increase of behavioural diversity. Shepherdson and colleagues (1993) did not discuss if their subjects performed abnormal behaviours during baseline conditions; knowing if there was a change in these would strengthen their conclusion that allowing the expression of natural behaviours improves captive animal well-being.

The motivation of captive animals to display foraging behaviours is supported by evidence that animals will ignore free food if given the opportunity to forage for it. This phenomenon is defined as contrafreeloading, occurring when animals work for food even when identical food is also freely available (Inglis et al., 1996). The following section provides an overview of contrafreeloading behaviour in the context of species displaying specific behaviours (e.g. foraging, exploration, physical manipulation).

### 1.3.6 Contrafreeloading

The first contrafreeloading report detailed how pigeons and rats pecked a disk or pressed a lever, respectively, to obtain a food reward while the same food was simultaneously freely available (Neuringer, 1969). Neuringer concluded that subjects were

performing a (learned) foraging behaviour, which they were motivated to display and were acting “naturally”.

Animals work for food to gain information about food sources and reduce their uncertainty (e.g. their location and palatability; Inglis et al., 1997) given the importance of this information towards their fitness (Woodworth, 1958; Inglis, 1987). Learning motivation and optimal foraging theories seem to be contradicted by contrafreeloading (Inglis et al., 1997) as these theories suggest animals should maximise rewards (Mazur, 2005) and minimise energy usage (Daniels and Burn, 2018), in other words, minimise the cost-benefit ratio (McFarland, 1977). This also applies to foraging behaviour, as natural selection is assumed to favour foraging strategies that maximise fitness (Pyke, 1984; McNamara and Houston, 1985). Contrafreeloading contradicts predictions from the optimal foraging theory indicating that animals should seek the greatest reward with the lowest effort (Inglis et al., 1997; but see Pyke (1984) and Pierce and Ollason (1987) for critiques on optimal foraging theory and Hummel et al. (2011) for an example in which sea stars *(Asterias rubens)* preferred small rather than large food items to avoid potential injuries). Inglis and colleagues (1997) proposed four explanations as to why captive animals may contrafreeload:

1) Because of secondary reinforcement associated with food dispensers and their delivery of food.
2) Due to prior training to obtain free or non-free food causing a neophobic response towards free food.
3) Stimulus changes related to non-free food are reinforcing and maintain contrafreeloading.
4) As a form of exploration or as self-assessment (in terms of their own foraging abilities) to gain information.
5) Because the behaviour performed to obtain non-free food is self-reinforcing.

Špinka and Wemelsfelder (2011) provided a rationale for contrafreeloading based on agency: “the propensity of an animal to engage actively with the environment with the main purpose of gathering knowledge and enhancing skills for future use”. In other words, animals perform behaviours (such as exploration in a foraging context) to gather information or achieve other goals apart from just satiating their hunger.

Contrafreeloading has been shown to be performed by a variety of species in diverse captive environments (Table 1.1), highlighting the apparent intrinsic need for some species to perform natural (foraging) behaviours in captivity (also discussed by Millar, 2010).

Table 1.1 – List of studies assessing the performance of contrafreeloading behaviour on captive animals. Adapted from Inglis et al., 1997.

| Species | Main finding | Reference |
|---|---|---|
| *Betta splendens* | Fish performed operant responses to gain access to a mirror image to perform display behaviour even when a free mirror was also available. | Baenninger and Mattleman, 1973 |
| *Columba liva* | Pigeons pecked a disk to gain access to grain while grain was freely available. | Neuringer, 1969 |
| *Gallus gallus domesticus* | Domestic fowl preferred to obtain food by pecking a disk than from a trough with ad libitum food. | Duncan and Hughes, 1972 |
| *Corvus brachyrhynchos* | Crows responded for food by pecking a cue even when free food was also available in a dish. | Powell, 1974 |
| *Sturnus vulgaris* | Starlings chose to obtain a high percentage of their diet by searching in covered holes rather than from an open dish; starlings contrafreeloaded by removing a membrane. | Inglis and Ferguson, 1986; Bean et al., 1996 |
| *Rattus norvegicus* | Rats pressed a lever for food pellets while free pellets were present. | Neuringer, 1969 |
| *Meriones unguiculatus* | Gerbils foraged for and ate seeds by digging in sand even when a bowl with seeds was also available; gerbils also work for seeds in different setups (with/without husks, glued to a stick) | Forkman, 1991; 1996 |
| *Macaca mulatta* | Rhesus macaques worked for food by solving a food puzzle when the same food was available in an open box. | Reinhardt 1994 |
| *Pan troglodytes* | Chimpanzees were tested on a discrimination task and subjects used this protocol to obtain food (even when they would have to score 100% on the task) even when free food was present. | Menzel, 1991 |
| *Sus scrofa* | Pigs expressed contrafreeloading in a test situation where finding and consuming food resembled natural foraging, as they foraged in a compartment where straw hid food reward when they could access another compartment also with straw but with food freely available in a trough. | Jonge et al., 2008 |
| *Chrysocyon brachyurus* | Wolves spent more than 50% of their foraging time in an area where food was scattered when compared to an area where food was presented in a tray. | Vasconcelos et al., 2012 |
| *Macaca fuscata* | Macaques were shown to press a button to receive visual stimulation in the form of a film even when a film was continuously being played in a different part of their cages. | Ogura, 2011 |
| *Ursus arctos horribilis* | Bears were found to forage by manipulating frozen food and boxes hiding food even when free food was also available. | McGowan, 2010 |

| | | |
|---|---|---|
| *Giraffa camelopardalis* | Giraffes foraged from a device requiring extra oral manipulations when feeders not requiring any additional manipulation were also available. | Sasson-Yenor and Powell, 2019 |
| *Bos taurus taurus* | Cattle were shown to push a gate to gain access to roughage even when free-to-access roughage was provided. | van Os et al., 2018 |
| *Psittacus erithacus* | Parrots obtained food dispensed by a foraging toy (puzzle feather) even when a free-to-access bowl was also available. | van Zeeland et al., 2010 |

The studies in Table 1.1 show how animals may have an intrinsic need to perform behaviours such as exploration or object manipulation in a foraging context. Following the discussion on behavioural needs and deprivation (Sections 1.3.4 and 1.3.5), not allowing animals to work for food (or other resources) may compromise their well-being. While some contrafreeloading studies included a training phase to allow subjects to learn how to work for food, others only provided a foraging task or device without any previous assessment on its relevance for the study subjects. If contrafreeloading species need to be provided with opportunities to work for food (e.g. foraging tasks or devices), research must be conducted to determine which characteristics influence the expression and level of contrafreeloading.

## 1.4 Research gaps and implications

This chapter presented a well-being definition in terms of animals being physiologically healthy, not suffering, showing positive affective states, and being able to display relevant behaviours. Also, three approaches to assess well-being were detailed: function, feelings, and natural living. Later, a behaviour-based approach to determine which species may fare better in captivity was described, followed by a description on how certain behaviours may be considered behavioural needs. Contrafreeloading was then introduced as evidence of this need.

Research on captive animal well-being appears biased towards settings and indicators associated with poor well-being (Yeates and Main, 2008). This biased focus, while not detrimental, limits well-being assessments. For example, an assessment that does not find indicators associated with poor well-being cannot conclude that subjects have good well-being. Ideally, information to assess well-being based on both negative and positive indicators should be available for all captive species. Given this bias towards negative indicators, the concept of “Positive Animal Welfare” (PAW) has been created to direct research towards including positive emotions and motivation associated to the provision of resources (Boissy et al., 2007; Yeates and Main, 2008; Lawrence and colleagues, 2019).

This thesis (Chapters 5 and 6) investigates preferred resources (i.e. what animals want) as these should induce positive affective states and improve well-being.

Other biases of well-being research relate to captive environments and model taxa. Hill and Broom (2009) commented on how most well-being studies involve farm animals, probably because of commercial interests. They also highlighted a gap in zoo-based research based on the higher number of species kept in zoos compared to those in farms. Melfi (2005, 2009) reviewed zoo-based research carried in British and Irish Association of Zoos and Aquariums (BIAZA) member zoos and found an evident bias towards using mammals (specially primates) as model species, with similar results reported by Stoinski et al. (1998) and de Azevedo et al. (2007). Melfi (2009) commented on how certain "rules of thumb" are created to compensate for this knowledge gap rather than following evidence-based approaches. To eliminate these biases and provide scientifically-sound guidance, research on less-studied captive taxa / species must be conducted.

The circa 360 recognised extant parrot species (Toft and Wright, 2015) form three groups: New Zealand parrots (Strigopoidea), cockatoos (Cacatuoidea) and all other parrots (Psittacoidea; Joseph et al., 2012). Parrots are commonly found in captivity, with the most common environments being zoos and households (van Hoek and ten Cate, 1998). Psittacine well-being research has focused on the Cacatuoidea (e.g. Jayson et al, 2014) and Psittacoidea (see Rodríguez-López, 2016) with no published studies discussing the well-being of captive Strigopoidea (apart from studies on managed wild populations of *Strigops habroptilus* e.g. Elliot et al., 2001). The next section introduces the kea[6] (*Nestor notabilis*), one of three extant members of the Strigopoidea, as the study subject of this thesis, highlighting their behaviour and cognition to formulate hypotheses about their well-being in captivity.

## 1.5 The kea parrot

Kea are part of the New Zealand parrot group, the most basal parrot clade, paraphyletic to all remaining parrots (Toft and Wright, 2015). Kea are endemic to the South Island of New Zealand (Diamond and Bond, 1999) living in habitats ranging from sea-level forests to altitudes above 1 km in the alps (Forshaw, 2010). Kea are currently listed as Endangered by the IUCN Red List, with a decreasing population of 4,000 mature individuals reported in the wild (BirdLife International, 2017) mostly due to lead poisoning and historic persecution.

[6] Kea, a Māori word, has the same form in singular and in plural.

Kea present sexual dimorphism, with males being usually bigger and having longer upper beaks (Diamond and Bond, 1999). Colouration helps determine the age of kea with fledglings having a bright yellow colour around their eyes, nostrils, and lower beak (Diamond and Bond, 1999). As fledglings grow older, the bright yellow colour starts fading until disappearing in adulthood (Diamond and Bond, 1999). Kea live as family groups composed of an adult pair and their most recent offspring. During feeding bouts, kea gather in small flocks of around 20-30 individuals.

Kea are omnivorous generalists. Their diet includes sap, seeds, berries and nuts from beech forests, but kea also visit landfills to look for food and even peck at sheep's backs to extract their fat (Diamond and Bond, 1999; Toft and Wright, 2015). In the wild, foraging and social behaviours are age-dependent, flexible, and interlinked. Diamond and Bond (1991) summarised these relationships: "the development of foraging can thus be seen as a transition from relatively non-social and indiscriminate exploring, to focused social interaction with adults, to attending mainly to the objects that adults control, and finally to focusing attention on the objects themselves".

Another behaviour that has been described in wild kea is play. Play behaviour is defined as any behaviour that: does not contribute to survival, is self-rewarding, has an "adult" equivalent, is repeated, and commences while being in a relaxed state (Held and Špinka, 2011). Play can be classified as: social (directed towards conspecifics), locomotor or object-oriented (see Held and Špinka, 2011), with these categories being non-exclusive. Kea have been reported to engage in "complex and persistent social play of variable patterns" (Diamond et al., 2006). Object-oriented play behaviour is also widespread in this species in both, solitary and social contexts (Diamond and Bond, 2004; Diamond et al., 2006). These behaviours often occur within large groups and for longer durations than its closest relative (the kaka, *Nestor meridionalis;* Diamond and Bond, 2004).

### 1.5.1 Kea in captivity

In New Zealand, kea's captive history dates to the 1960s (Pullar, 1996). While wild kea have been reported to have a lifespan of 7-10 years (e.g. Meehan, 2017), captive kea have a median lifespan of 2.8 years (N= 773) but this median increased to 10.4 (N=339) when filtering out juvenile (i.e. less than four years) mortality (Young et al., 2012). In the wild, juveniles also have high mortality rates with more than 60% perishing before their first year (Akers and Orr-Walker, 2009). Juvenile mortality in the wild appears associated with predation and poisoning (van Klink and Cromwell, 2015). In captivity, there is no clear

evidence for the causes of juvenile mortality, but captivity should prevent predation and poisoning from happening, indicating that other causes should exist.

There are no published studies that assess the well-being of captive kea. There is a husbandry report mentioning one kea, of undisclosed age, dying of enteritis after 25 years in captivity, and another dying after 31 years in captivity with evidence of pulmonary sclerosis, myocardium degeneration and enteritis (Schmidt, 1971). This same report also provided an account of the reproductive success of all kea kept in Zurich Zoo from 1959 until 1970: eight clutches were laid in this period, resulting in twenty-four chicks hatching from 31 eggs. There is no information on post-hatchling survival besides mention of one egg found broken in the enclosure and one chick dying on the day it hatched with no further explanation. A second husbandry report from a UK institution mentioned three kea pairs producing 106 chicks between 1983 and 2000, with 62 chicks raised to independence (Woolcock, 2000). Some of the causes for chick mortality included: nest abandonment, nests being invaded by ants and *Escherichia coli* infection. This report also mentioned one adult kea that lost her entire upper mandible from unknown circumstances, but she was reported to have no difficulty eating and still took part in feeding chicks (Woolcock, 2000). A short communication by Bakonyi and colleagues (2015) described the infection of a group of captive kea with West Nile Virus. Eight kea from a flock of 24 birds showed clinical signs consisting of loss of appetite, lethargy, crouching and hanging heads while resting and fluffed head feathers. One bird was euthanised due to the severity of its neurological signs. The remaining birds recovered but showed clinical signs in subsequent years but after six years all five kea had been euthanised. Authors concluded that kea appear highly susceptible to West Nile virus infection “with an unusual clinical course”. There is also an old record showing that *Chlamydia psittaci* was isolated from kea (Johnson et al., 1984).

The previous reports provide contradicting well-being conclusions. Kea’s health appeared compromised (Schmidt, 1971; Bakonyi et al., 2015), which the function-based approach recognises as poor well-being. However, kea were reported to successfully reproduce (Schmidt, 1971; Woolcock, 2000), recognised by the same function-based approach as good well-being (but see Section 1.2.1 for an example in which breeding output may not indicate good well-being). The only clear conclusion is that research on the well-being of captive kea is lacking besides these descriptive and outdated reports based only on physiological and reproduction indicators.

There is a body of literature on both wild and captive kea that explored their physical and social cognition. These studies are briefly described next as a starting point to discuss

behaviour-based well-being (see “behavioural needs”, Section 1.3.4) and to indicate why kea were considered as the focal species for the present research project.

### 1.5.2 Research on kea cognition

Kea have been common test subjects in studies about cognition, problem-solving, and cooperation. Research in the wild showed that when solving a novel foraging task (opening the lids of rubbish bins), only 5 out of 36 kea were successful, with most subjects benefitting from being scroungers (Gajdon et al., 2006). Authors concluded that social learning did not occur in this foraging context. A separate study (Huber et al., 2001) found that, in captivity, kea showed social learning, as evidenced by an increase in the efficiency to open a food container by kea who observed a skilled conspecific perform the same task. These differences between wild and captive kea were also reported by Gajdon and colleagues (2004). In their experiments, wild and captive kea were exposed to a foraging task which required individuals to release food by climbing a pole and sliding a container until it detached from the top end. Wild kea found the task difficult, with only 3 out of 21 subjects succeeding. A small sample of captive kea appeared more proficient, as 3 out of 5 birds solved the task when tested in isolation. Authors concluded that these differences were probably related to the experimental experience of the captive kea but also discussed how exploration behaviour, assumed to be relevant to solve the task, appeared consistent in duration between wild and captive kea (Johnston, 1999).

Research on technical cognition showed that kea were able to: navigate a tool to access a food reward even as non-tool users in the wild (Auersperg et al., 2011a), access a food reward by solving up to four different tool-use techniques, showing more exploration than New Caledonian crows (*Corvus moneduloides*) (this was the first account of psittacine tool-use in captivity; Auersperg et al., 2011b), successfully solve a second-order (i.e. two-step) tool task by inserting a ball into a pipe to release a food reward (Auersperg et al., 2010), rely on exploration to open different lock configurations (Miyata et al., 2011), and showed higher success rates when solving tool-based tasks (dropping a weight or inserting a rope to retrieve food rewards) after being allowed to explore objects relevant to the task (Lambert et al., 2017). Captive kea were also found to solve a foraging task consisting of choosing one (rewarded) tube out of two differently-shaped options by exclusion performance[7] but failed to solve another foraging task consisting on choosing one (rewarded) bowl out of two identical options when exclusion performance was forced by the experimenter (Schloegl et al., 2009). Kea and ravens (*Corvus corax*) were tested in this

[7] Exclusion performance occurs when one alternative is chosen by excluding the alternative option, see Call, 2006.

exclusion performance experiment and only ravens successfully solved both tasks. This was "the first study to demonstrate that corvids and parrots may perform differently in cognitive tasks" (Schloegl et al., 2009). O'Hara et al. (2016) also tested kea on an inference by exclusion paradigm via a visual discrimination task. Kea were first trained with many novel stimuli to discourage their explorative behaviour towards novel stimuli. After training, kea were tested by allowing them to choose either rewarded or unrewarded cues paired with novel cues. Kea were found to infer by exclusion, but their choices also included instances of novelty aversion, one-trial learning, stimulus preferences (i.e. bias) and avoidance. Kea were also found to differentiate tool affordances in a foraging task by discriminating between functional and non-functional cues (Auersperg et al., 2009). Schwing and colleagues (2017b) showed that kea displayed forward planning and economic evaluation based on their differentiation between preferred and non-preferred rewards and their waiting times in a food exchange paradigm. O'Hara and colleagues (2015) also showed that kea were able to discriminate and succeed at reversal learning at a faster rate when the associated stimuli are tangible objects rather than 2D images on a display.

### 1.5.3 Behaviour-based predictions for the well-being of kea in captivity

Following the rationale of Section 1.3, kea have certain behavioural traits that indicate their well-being should not be compromised in captivity (see Mason, 2010). In terms of boldness, kea are highly curious, explorative, and destructive, factors that help them survive in their natural habitat (Diamond and Bond, 1999). Captive kea also rely on explorative behaviour to successfully solve certain tasks (see Section 1.4.2). Given their boldness, kea should fare well in captivity. Similarly, kea should readily adapt to new environments (and, potentially, to captivity) due to their non-migratory lifestyle. However, kea display opportunistic foraging behaviour, which enables them to maximise habitat exploitation and restricts the conquering of new habitats (Huber and Gajdon, 2006). Given the kea's full adaptation to the alpine environment, there is a possibility that their well-being could be compromised in new or different environments, including captivity. In terms of behavioural flexibility, the foraging behaviour of wild kea has been described as flexible (Diamond and Bond, 199) and captive kea have been shown to be flexible problem-solvers (Auersperg et al., 2011). This behavioural flexibility also implies kea should fare well in captivity.

The reports on kea mortality and reproductive success discussed in Section 1.5.1 suggested that the well-being of captive kea may be compromised. Unfortunately, there are no scientific studies assessing the well-being of captive kea. To produce evidence-based

predictions on kea's well-being, a comparative route can be followed by reviewing the well-being literature of closely related species.

## 1.6 Captive parrots: an overview

Parrots are often found in captivity across different environments: in zoos to aid in their conservation, as pets for companionship (van Hoek and ten Cate, 1998), and in non-zoological research facilities (Kalmar et al., 2010). Estimates indicated that there are 10 million pet parrots in the United States (Kalmar et al., 2010), 5 million pet parrots in the Netherlands (Roe, 1991) and 5 million pet budgerigars (*Melopsittacus undulatus*) in the United Kingdom (Roe, 1991). Furthermore, there was an estimate of 3 million captive parrots in Belgium and 45 million in the rest of Europe (based on a personal communication, Kalmar et al., 2007). Up to 2009, there were more than 20,000 parrots housed in zoos worldwide (ISIS, 2009). Information on the number of parrots kept in research facilities is not available, but a review on psittacine publications only in 2009 found 483 laboratory parrots (Kalmar et al., 2010).

Kalmar and colleagues (2007) argued that all captive parrots should be treated as wild, given that most are either wild-caught or from an early generation (but Webb and colleagues (2010) consider a "handful", unnamed, parrot species to be domesticated). This short captive history may hinder adaptation to captivity, since animals adapt after more than one lifespan (Kalmar et al., 2007). This consideration could have an impact on parrot well-being, as the behavioural needs of domestic versus wild species are not always the same (e.g. dogs and wolves in Marshall-Pescini et al., 2017).

### 1.6.1 The well-being of captive parrots

The literature on parrot well-being is not as extensive as other avian species. Web of Science returns 1967 results (as of September 2019) when searching for "welfare" and "birds" under "topic", but only 74 when "birds" is replaced with "parrots". More than 260 parrot species have been kept in captivity (Young et al., 2012), representing more than 71% of the extant parrot species (Forshaw and Knight, 2006). Rodríguez-López (2016) named 21 parrot species used as subjects in well-being studies. This disproportion shows that knowledge on parrot well-being is insufficient. Nonetheless, this limited set of studies provide insight into psittacine well-being.

The following discussion summarises some examples of how the well-being of captive parrots appears to be affected by captive conditions (originally listed by Meehan and Mench, 2006). This overview is provided as a comparative approach to determine well-being

predictors for kea. Lastly, studies that have tried to minimise or eradicate these well-being problems are discussed, also expecting to gain insight into which opportunities may be relevant for kea.

#### 1.6.1.1 Stereotypies

Meehan and Mench (2006) recognised three types of stereotypies performed by parrots: oral (e.g. spot pecking, sham chewing, bar biting, tongue rolling), locomotor (route tracing and pacing), and object-directed (repetitive, invariant manipulation of objects). Oral and locomotor stereotypies have been reported to be widespread amongst captive parrots housed in barren conditions (e.g. 96% of a laboratory-housed colony performed these behaviours, Meehan et al., 2004; Garner et al., 2006). Captive budgerigars (*Melopsittacus undulatus*) displayed oral (wire and sham chewing), locomotor (pacing and route-tracing) and objected-directed (spot-pecking, mating feign, and incessant screaming) stereotypies significantly more when housed as pairs in small cages than when socially housed in larger cages (Polverino et al., 2012). Individually housed Amazons (*Amazona amazonica*) performed more stereotypies (pacing, perch circles, corner flips, route tracing, wire chewing, sham chewing, food manipulation, and dribbling) when they were surrounded by more conspecifics (Garner et al., 2006). Amazons (*Amazona aestiva*) performed less abnormal behaviours (misdirected pecking, stress vocalisations and pacing) when their environments were made more complex (by increasing foraging and exploration of opportunities; Amorim and Schetini, 2011).

#### 1.6.1.2 Feather damaging behaviour

Feather damaging behaviour (FDB) is another abnormal behaviour displayed by parrots consisting of chewing, biting, and/or plucking their own feathers and/or skin, often resulting in damaged feathers or skin injuries (Harrison, 1986; Rosskopf and Woerpel, 1996). This behaviour appeared widespread in the captive parrot population with an estimated incidence of 10% (assumed by consensus in Grindlinger, 1991). In parrots, this behaviour is, in most cases, self-directed, which contrasts to other captive bird species. For example, laying hens are also reported to engage in FDB consisting of pecking and pulling out feathers of cage-mates (Van Zeeland et al., 2009). This contrast is suggested to be a consequence of the social conditions in which these species are kept, with parrots often being housed individually and laying hens being housed socially (Meehan and Mench, 2006).

The aetiology of FDB is still under debate but research has theorised several explanations, including FDB being: “habitual” (Johnson, 1987), intensified grooming patterns

(Harrison, 1986) or “redirected foraging” behaviour (Meehan et al., 2003). Meehan and Mench (2006) suggested redirected foraging behaviour as a plausible explanation, based on evidence from other avian species. For example, chickens display FDB when pecking behaviour (required to forage) is inhibited by providing slatted floors (Blokhuis, 1986) but when non-food-based pecking opportunities are provided, FDB is reduced and prevented (Huber-Eicher & Wechsler 1997). A study on parrots supported this theory as parrots performed less FDB when given additional opportunities to forage (Meehan et al., 2003) but subjects simultaneously received items that encouraged exploration and manipulation outside of a foraging context, thus confounding the results. This confounder was not present in a separate study by Lumeij and Hommers (2007) as they provided captive parrots exclusively with additional foraging opportunities and these were effective at reducing the performance of FDB.

FDB has also been speculated to be caused by several other intrinsic and extrinsic factors such as: social environment, physical environment, neurobiological factors, genetic factors, and medical problems (van Zeeland et al., 2009), but research on these is limited apart from one study finding a genetic basis for FDB (Garner et al., 2006) and one finding a reduction in FDB as a result of increasing environmental complexity (Meehan et al., 2003).

#### 1.6.1.3 Health and reproduction

Doneley (2009) described bacterial infections and parasitic diseases found in pet parrots because of increased pathogen loads attributable to the close confines of captivity. Donely noted that the detection of bacteria may not be indicative of a well-being compromise as they may be part of parrots’ “resident flora” or simply “transitioning through the bird”. Parasitic loads may result in death or diseases or they may have no health effects. Some of the bacterial pathogens and their effects on parrots are listed in Table 1 of Doneley’s study, including their source and site of infection. Out of these 14 examples, 7 originated from husbandry-related factors such as contaminated food and water and contact with other species (e.g. vermin). Doneley noted that there is a time effect on parasitic and bacterial infections, commenting on how wild-caught birds often presented a high occurrence of infections, which has been found to decrease with veterinary advances. *Chlamydophila psittaci*, a bacterium whose clinical signs include anorexia, dyspnea, dehydration, diarrhoea, weight loss, conjunctivitis, rhinitis, and sinusitis (Gerlach, 1984) has been found to be prevalent in the captive populations of Amazon parrots (95 individuals from eight different *Amazona* species, de Freitas Raso, 2002).

There is only one published study assessing the physical health of captive parrots based on environmental parameters. Meehan and colleagues (2003) housed 21 Amazons

(*A. amazonica*) according to two treatments: singly housed or iso-sexual pairs. These housing conditions were kept for 12 months, during which the behaviour of the subjects was recorded. Three injuries were observed during the study: two of these were not fully described besides mentioning that they occurred in the first month to two pair-housed subjects (non-cage mates); the third injury was a wing abrasion in a paired parrot. No injuries were reported on singly housed parrots, suggesting that social housing could have a negative effect on well-being. Meehan and colleagues (2003) claimed that the three injuries were not a result of intra-pair aggression but did not discuss other probable causes. Also, five parrots (three paired subjects and two singly housed) showed clinical signs of infection with *Bordetella avium*. There were no cases in which two cage mates showed clinical signs of this pathogen (but authors explain some birds could be infected and asymptomatic). Again, social housing was discussed as not having a negative effect on well-being based on the low frequency of infected cases.

Following the biological functioning component of well-being, impaired reproduction, negatively affecting fitness, may also show a negative effect on well-being. Some parrot species showed lower hatch rates or no breeding behaviours when kept in captivity (see Allen and Johnson, 1991; Schubot et al., 1992; Juniper and Parr, 1998) while others appeared to readily breed in captivity (see Clubb, 1992; Derrickson and Snyder, 1992). However, using reproduction as a well-being indicator may be unsuitable, as animals kept under conditions associated with other well-being problems still reproduce (Fraser and Broom, 1990; Fumarola, 1998).

#### 1.6.1.4 Other behaviours

The literature on pet parrots recognised other behaviours as indicators of parrots not coping with their environment such as aggressiveness, fearfulness and screaming (Meehan and Mench, 2006). The reason these behaviours were assigned to a poor well-being state is due to owners' opinions. Constant screaming was surveyed as the second most common complaint of parrot owners (Kidd and Kidd, 1998) but this just means that the behaviour is problematic for the human owner. While there is evidence that loud vocalisations correlated with other factors associated with poor well-being (e.g. Boinski et al., 1999), reports on parrots do not rely on scientific evidence, commenting on how "a well-trained bird […] quietly observes the interaction" and "some pets scream because they are angry at a situation" (Davis, 1991). A starting point to adequately determine if loud screaming is abnormal would be to measure the vocal patterns (e.g. sound intensity) of wild parrots (e.g. Martella and Bucher, 1990) and compare these to captive conspecifics, but no study has attempted to perform this comparison.

Aggression and fear responses have also been associated with poor well-being. As described by Broom (1991a), fear occurs when a dangerous situation is predicted or is occurring. Fear has been described to be an undesirable emotion (Jones, 1997); when in a fearful state, animals also displayed behaviours such as a violent escape response that can cause injuries or death in the captive environment (Jones, 1996). Research on captive parrots has shown that when housed in barren environments, parrots appear more fearful, as quantified by the time they took to approach a novel object (Meehan and Mench, 2002). As with extreme vocalisations, hyper-aggressiveness is also considered negative due to the opinion of parrot owners, as aggressive parrots are "more difficult to care for" (Meehan and Mench, 2006). The relevance of aggression in terms of well-being results from cases in which socially housed animals fight and these interactions, unavoidable due to confinement, result in injuries (e.g. Giersing and Studnitz, 1996). Some species even show self-injurious behaviour (i.e. self-aggression) that is performed under stressful conditions and results in injuries (e.g. Hosey and Skyner, 2007; Britt et al., 2015).

The preceding sections showed how captivity may negatively impact the well-being of captive parrots, mostly based on parrots' health and behaviour. There is an approach that tries to improve the well-being of captive animals: environmental enrichment (hereafter enrichment). The following discussion defines and describes this approach, keeping parrots as a reference taxon to try to find suitable opportunities for kea.

### 1.6.2 The environmental enrichment approach

One of the earlier definitions of environmental enrichment describes it as "an improvement in the biological functioning of captive animals resulting from modifications to their environment" (Newberry, 1995). Early enrichment research focused on analysing the behavioural effects of differential living quarters. Most of these pioneering studies were conducted in laboratory settings with rodents as subjects and with the objective of comparing rodent behaviour in two types of environments: barren cages including minimal stimuli (e.g. food, water and bedding) and "enriched" cages, often larger in size and including a vast array of furniture and toys, but their well-being discussions were lacking (e.g. Manosevitz et al., 1968; Bennet et al., 1969; Henderson, 1970; Manosevitz, 1970; see Fox, 2006 for a review).

The definition of enrichment was modified and expanded by Shepherdson (1998). He replaced "environmental modifications" with "husbandry practices" and the former "improvement in the biological functioning" with an optimisation of "psychological and physiological well-being", thus aligning with the feelings-based well-being approach (see Section 1.2.2). This revised definition came with a broadening of the scope of enrichment

research, expanding from laboratory environments to include other captive settings such as farms and zoos.

Farm animals are subjected to specific management practices as they must follow industry requirements and maximise economic benefits for the producers. Intensive breeding in barren conditions was common in historic farm animal management. However, consumers' interest in the well-being of animals has influenced the keeping and husbandry of farm animals. Just in Europe, legislation was set in place to prohibit battery cages for laying hens, mostly because of public interest in improved animal well-being (Jones, 2004). This led to an increased interest in determining proper housing parameters. For example, Hocking and Jones (2006) included string and wood shavings bales in the environment of hens, finding that aggression and feather damaging behaviours were positively affected by these items. Another example occured with mink (*M. vison*) research, with studies including enlarged habitats fitted with resting areas and toys (Hansen et al., 2007) or a swimming opportunity (Vinke, 2005), finding that abnormal behaviours decrease in such environments.

The improved environments described above included certain objects or resources, which are classified as enrichment. Enrichment opportunities are often categorised into one (or more) of the five enrichment types named by Bloomsmith and colleagues (1991) and Young (2003) based on the type of stimuli provided:

- Social enrichment when conspecifics or human interaction are provided as stimuli,
- Occupational enrichment when behavioural responses are elicited without relying on food rewards,
- Physical enrichment if the living quarters are changed in terms of size, complexity, or furnishings,
- Sensory enrichment if visual, auditory, tactile, or olfactory stimuli are provided,
- Nutritional enrichment if food type or its delivery method was part of the experimental protocol.

This categorisation is useful as it distinguishes between specific stimuli, enabling systematic evaluations and allowing animal caretakers to supply a variety of opportunities according to their needs and resources. However, these categories are often non-exclusive, as many enrichment opportunities mix different stimuli or rewards. For example, zoos often train captive animals to facilitate good animal care (e.g. Colahan and Breder, 2003), which Melfi (2013) described as enriching, as training resulted in improved biological functioning (due to medical care) and allowed the expression of specific behaviours. A common training technique is positive reinforcement, in which a trainer (human) uses rewards (e.g. food) to promote the expression of desired behaviours (Hiby et al., 2004). The human-animal

interaction would classify as social enrichment while the provision of a food reward would classify as nutritional enrichment. Melfi (2014), however, discussed how training is not a type of enrichment as these differ in “process, outcome and function”. There also appears to be a conflict between occupational and physical enrichment, recognised by Millar (2013), as providing physical enrichment such as furniture resulted in animals performing certain behaviours pertaining to the goals of occupational enrichment. Millar proposed a re-classification of enrichment types merging physical and occupational enrichment and including a new, recent category: cognitive enrichment.

The concept of cognitive enrichment originated with the provision of specific occupational and foraging opportunities to farm animals. “Cognitive enrichment” is defined as “the ability to elicit perceptive processes or operant learning of discriminatory cues which lead eventually to a better active control of the environment” (Manteuffel et al., 2009). Cognitive enrichment has also been discussed in relation to contrafreeloading, as cognitive enrichment protocols often allow for the performance of behaviours related to working for food.

Experiments looking into the well-being effects of cognitive enrichment include operant tasks with auditory or visual discrimination components that, when properly solved, provide subjects with food or water. A study where goats were able to obtain water by solving a visual discrimination task showed a preference for this task (as water was available from a second apparatus requiring pushing a button sans discrimination task; Langbein et al., 2009). Another experiment where pigs were given an auditory discrimination task to obtain food showed the well-being effects of these tasks: pigs were less aggressive, less fearful and their heart rate decreased (Zebunke et al., 2013). One must keep in mind, however, that the desired effects on well-being still have to comply with the farmers’ interests, thus favouring some behaviours over others (e.g. less fearful or aggressive animals may be easier to manage). Studies on primates (Brent and Eichberg, 1991; Gilloux et al., 1992; Clark and Smith,2013) and cetaceans (Clark et al., 2013) have designed and implemented mazes and puzzle feeders to target cognitive abilities. These mazes were found to increase social play and tool-use (Clark and Smith,2013); reduce aggression, affiliation, inactivity, and negative, self-directed behaviours (Brent and Eichberg, 1991); increase food-oriented behaviours (Gilloux et al., 1992); and increase vigilance and time spent underwater (Clark et al., 2013).

Most research on psittacine enrichment investigates changes in different behavioural categories and interprets these as improving (or worsening) their well-being. The validation for this approach comes from the naturalistic well-being viewpoint, which considers

opportunities to exercise naturalistic behaviours such as exploration, foraging and locomotion as good well-being (Cubas et al., 2006; see Section 1.2.3). Table 1.2 presents a brief overview of the parrot species, experimental protocols, and conclusions of the existing enrichment studies on parrot well-being.

Table 1.2 – Enrichment studies using captive parrots as subjects. The number before the species is the sample size. Adapted from Rodríguez-López, 2016.

| Subjects | Experimental protocol | Behavioural measures | Well-being conclusion | Reference |
|---|---|---|---|---|
| 18 *Nymphicus hollandicus* | Provision of wooden sticks or iron rings | Naturalistic ethogram + "undesirable behaviours" | General positive effect due to the reduction of "undesirable behaviours" | Assis et al., 2016 |
| 2 *Anodorhynchus leari* | Provision of foraging and physical opportunities | Naturalistic ethogram + abnormal behaviours (pacing and feather picking) | General positive effect due to increased natural activity and decreased abnormal behaviours | Azevedo et al., 2016 |
| 36 *Melopsittacus undulatus* | Differential housing: pairs vs. group; small vs. large cages | Species-specific ethogram + abnormal behaviours (oral, locomotor and object-directed) | Smaller cage size increased frequency of abnormal behaviours; social housing reduced the frequency of locomotor stereotypies | Polverino et al., 2015 |
| *1 Amazona oratrix*<br>*2 Psittacus erithacus*<br>*1 Anodorhynchus hyacinthinus*<br>*2 Ara macao*<br>*2 Ara militaris*<br>*2 Ara ararauna* | Provision of auditory stimuli; rearing method and social environment added to statistical analyses | Species-typical ethogram + stereotypies (feather-plucking, locomotor, oral, bar biting) | Auditory stimuli only affected preening and vocal behaviour; hand-rearing subjects performed more stereotypies than parent reared; solo-housed parrots performed more stereotypies than group-housed | Williams et al., 2016 |
| 16 *N. hollandicus* | Provision of collard green stalks | Ethogram from another parrot species | Protocol reduces sleep behaviour which authors associate with reduce idleness and potentially less undesired behaviours | Carvalho et al., 2017 |
| 2 *Guaruba guarouba* | Provision of foliage, fruits, nuts, etc. (full list of items not included) | Species-specific ethogram + feather plucking | Item provision affected rest, exploration, locomotor, vocalisation, and preening behaviours; feather plucking not eliminated, protocol potentially beneficial as increased activity associated with decreased feather plucking | Clyivia et al., 2015. |
| *4 Ara rubrogenys,*<br>*2 Rhynchopsitta pachyrhyncha,* | Provision of two foraging devices | Ethogram of unknown origin lacking abnormal behaviours | Positive effect from the foraging devices due to increase in foraging and preening behaviours | Coulton et al., 1997 |

| | | | | |
|---|---|---|---|---|
| *2 Ara cloroptera, 2 Lotius garrulus* | | | (preening also discussed as a potential negative effect) | |
| 12 *A. amazonica* | Relationship between bathing behaviour and activity budgets | Species-specific ethogram developed in the study | Inducing bathing behaviour allows the expression of species-specific, natural behaviours | Murphy et al., 2011 |
| 10 *Amazona aestiva* | Provision of foliage, branches, fruits, seeds, leather items | Species-specific ethogram including pacing and abnormal pecking | Positive effects based on promoting foraging and exploratory activities and decrease of abnormal pecking | de Andrade and de Azevedo, 2011 |
| 64 *A. amazonica* | Analysis of genetic, environmental, and social factors | General ethogram and stereotypies based on a species-specific pilot study | Feather-picking appeared hereditary; number of neighbouring birds affected stereotypy levels | Garner et al., 2006 |
| 21 *A. amazonica* | Effects of same-sex housing on well-being | General and stereotypical behaviours; only the latter with previous reference on species-specific research | Paired parrots preened less and were more active than singly housed birds. Pair-housing had a positive impact on well-being as none of these birds developed stereotypical behaviours (57% of singly housed birds did) | Meehan et al., 2003a |
| 10 *Pyrrhura perlata perlata* | Provision of food, toys, and perches | Species-specific ethogram with a focus on feather-picking | Feather-picking conures were more stationary, preened, allo-preened, and interacted with conspecifics more than non-feather-pickers. Item provision stabilised plumage condition but did not improve it | van Hoek and King, 1997 |
| 64 *A. amazonica* | Provision of non-described foraging and physical opportunities; also analysed the social environment | Abnormal behaviours | The study design did not allow to assess the effect of foraging and physical enrichment; but parrots with more neighbour birds displayed less abnormal behaviours | Garnet et al., 2006 |
| *2 Ara ambiguus, 2 A. cloroptera* | Behavioural training for artificial insemination procedures | General behavioural activity and stereotypical behaviours | Training did not result in stress or affected reproductive behaviours of both *A. ambiguous*; female *A. chloroptera* showed signs of stress; male *A. chloropterus* did not complete training. | Leblanc et al., 2011 |
| *14 Trichoglossus ornatus* *10 Charmosyna josefinae* | Novel object exploration tests comparing resident versus nomadic | Latency to touch novel object, number of objects touched and duration of exploration | Resident species showed earlier exploration which was positively | Mettke-Hoffman, 2000 |

| | | | | |
|---|---|---|---|---|
| *12 Charmosyna pulchella pulchella*<br>*14 Psephotus dissimilis*<br>*12 Trichoglossus haematodus moluccans*<br>*14 Psephotus varius*<br>*14 Neopsittacus pullicauda*<br>*14 Charmosyna papou goliathina*<br>*14 Northiella haematogaster*<br>*14 Psephotus haematonotus* | species and feather plucking behaviour | | correlated with feather-plucking | |
| 18 *P. erithacus* | Provision of pipe feeders | Foraging and feather damaging behaviours | Pipe feeder increased foraging time and feather condition | Lumeij and Hommers, 2008 |
| *16 A. Amazonica* | Increased cage physical complexity and supplied foraging enrichment | Behavioural responses towards novelty and human handlers; feather damaging behaviour; development of stereotypical behaviours | Enrichment opportunities reduced fear responses; reduced feather damaging behaviour; and nearly prevented the development of stereotypical behaviour. | Meehan and Mench, 2002; Meehan et al., 2003b; Meehan et al., 2014 |
| *48 Nandayus nenday* | Physical and social enrichment | Fear and exploratory behaviours | Enrichment protocols reduced fear levels and increased exploration in some tests | Luescher and Sheehan, 2005 |
| 6-*12 A. amazonica* | Foraging enrichment | Analyses of foraging behaviour and preferences | Oversized pellets made foraging times like wild activity; parrot appetites motivated by food form | Rozek et al., 2010 |
| *13 A. amazonica* | Variety of physical foraging and social enrichment by handlers | Abnormal behaviours | Enrichment deprivation decreased feather condition and increased time spent stereotyping | Cussen and Mench, 2015 |
| 12 Aratinga leucophthalma | Several items of sensory, foraging and physical enrichment | Feather damaging behaviour | Enrichment more effective in treating feather damaging when compared to a drug treatment | Telles et al., 2015 |
| *12 A. amazonica* | Rope varying in colour and size | Preferences for assorted colours and lengths | Parrots showed sex-specific preferences, with females preferring wound | Webb et al., 2010 |

| | | | | |
|---|---|---|---|---|
| | | | rope, males interacting for longer durations and both sexes preferring more red rope. | |
| *10 A. amazonica* | Foraging and physical enrichment | Preferences for pellet types and objects | Bigger pellet sizes may allow parrots to perform naturalistic foraging behaviour | Rozek and Millam, 2011 |
| *8-10 A. amazonica* | Cubes varying in colour and material | Preferences for assorted colours and materials | Parrots preferred yellow and orange cubes, cubes of smaller sizes and cubes made of softer materials | Kim et al., 2009 |
| *6 Calyptorhynchus banksii* | Foraging interventions (e.g. scattered food items, feeders) | General behaviours (e.g. resting, foraging, locomotion, maintenance, oral stereotypies) | Foraging enrichment increased foraging times and decreased oral stereotypies | Fangmeier et al., 2019 |
| *16 A. araruna*<br>*2 A. macao* | Foraging, physical, and occupational enrichment | General behaviours (e.g. locomotion, inactivity, foraging, maintenance, allopreening, social interactions) | Foraging enrichment elicited higher interaction rates; all enrichments changed parrots' behavioural repertoire | Reimer et al., 2016 |

Most methodologies of the psittacine enrichment studies described in Table 1.2 are based on the development of an ethogram (i.e. behavioural catalogue) that is completed under two or more different conditions. These two conditions are, in most cases, a non-enriched (i.e. barren or deprived environment or lack of stimuli) and an enriched (i.e. objects, toys or other stimuli provided) phase. Most studies used foraging or physical stimuli in the form of (puzzle) feeders, extra food, toys, and other objects that were expected to increase foraging behaviours during the enriched phase. Studies providing sensory enrichment are less common, but there is evidence that sensory-based stimuli may be effective in modulating abnormal behaviours (e.g. Telles et al., 2015). There are no published studies providing or evaluating cognitive enrichment to captive parrots.

Some studies (e.g. Assis et al., 2016; Carvalho et al., 2017) included in their aims the reduction of "undesirable behaviours", which does not necessarily correspond with poor well-being (see Engebretson, 2006 and Section 1.5.1.4). Another limiting factor present in several studies is that they constructed their own ethogram based on baseline, non-enriched conditions. This could limit the interpretation of results, since it established the baseline phase as a well-being reference without identifying it as poor or good. Some studies have circumvented this drawback by also analysing other behaviours or parameters that are

already known indicators of poor well-being (e.g. feather-picking and stereotypical behaviours).

Research on captive parrot well-being (Table 1.2) appears to follow the functional approach (research on abnormal behaviours) and, to a lesser extent, the naturalistic approach (studies comparing foraging times to those of wild conspecifics). The “feelings” approach appears less common, with studies determining parrots’ preferences for certain materials and colours (e.g. Webb et al., 2010; Kim et al., 2009), and for pellet sizes (Rozek et al., 2010).

## 1.7 Concluding remarks

This Chapter illustrated how captive animals adapt to their manufactured environments, highlighting the effects on their well-being and the different ways to measure if they are coping with their environments. This discussion also emphasised how some behaviours are intrinsically motivated and when their expression is constrained, well-being may be negatively impacted. Contrafreeloading was presented as an example, noting how captive animals work for (food) resources by interacting with a variety of devices or performing different foraging behaviours.

As discussed in Section 1.4, well-being research appears biased towards mammalian species, with less work focusing on other taxa. Parrots were discussed as a taxon that has received less attention in terms of well-being research, though some studies have reported negative effects and attempts to minimise them. The kea was then introduced as the study subject of this thesis, mentioning its captive history, the lack of knowledge on its well-being and emphasising its wild ecology and cognitive abilities as factors that should be considered when housed in captivity. This does not mean that kea are behaviourally and/or cognitively “superior” to other species and, consequently, more deserving of the role of study subjects. However, cognitive skills are recognised as a requirement to forage, mate and avoid predators (Shettleworth, 2010) and exploratory behaviour has been recognised as an important tool to deal with challenges (Meehan and Mench, 2007). The relevance of exploration is such that some species have been shown to contrafreeload, a phenomenon that has been interpreted to indicate that “animals enjoy doing things and exerting control over their environment” (Markowitz, 1982).

While under Mason’s (2010) framework kea do not seem susceptible to poor well-being in captivity, their neophilia and exploration could be considered characteristics that should be catered for in the captive environment. As per Section 1.3.5, depriving captive kea of these behaviours could be a potential well-being risk. Furthermore, anecdotal

observations of captive kea by the researcher found that they are susceptible to developing abnormal behaviours such as stereotypies. Parrot well-being studies appeared focused on specific indicators such as abnormal behaviours, and ways to improve their well-being in terms of environmental enrichment. Less attention has been given to determining the preferences and motivations of captive parrots.

The knowledge gaps identified in this Chapter have led to the formulation of specific research objectives that attempt to understand the status of captive kea in terms of husbandry and management, and to determine viable options to improve their captive environment by understanding which factors could enable the performance of species-specific behaviours (**natural-living** well-being approach). As initially worded by Meehan and Mench (2006), the researcher intends to determine elements that are important for normal behavioural development and that also satisfy kea's preferences (both relevant from the **function** and **feelings** well-being approaches).

## 1.8 General research objectives

***Objective 1: Obtain information on the status quo of the management, husbandry and behaviour of captive kea and appraise these in terms of well-being***

The first goal of this thesis was to collect quantitative data on the husbandry practices of international kea holders and to compare if these were in accordance with management guidelines. Also, the occurrence of behaviours associated with negative well-being in parrots was investigated in captive kea. Zoo surveys are a popular tool to collect data from multiple sources and large sample sizes (e.g. Eriksson et al., 2010; Morabito and Bashaw, 2012; Rowden and Rose, 2016). Thus, an online survey was created and distributed with questions about the physical environment (i.e. enclosure), feeding and enrichment routines and abnormal behaviour. Collected data were analysed and used as explanatory variables in a model predicting the occurrence of abnormal behaviours to determine if there is indeed a well-being effect of the husbandry recommendations. This result would function as evidence for these recommendations, currently lacking in kea.

***Objective 2: Evaluate specific management / husbandry practices in terms of behaviour-based well-being***

Section 1.6.2 introduced the concept of environmental enrichment as a common tool in parrot studies to improve well-being by behavioural changes. Most enrichment studies on parrots used physical or foraging interventions and these have been shown to have a positive effect on parrot well-being (Rodríguez-López, 2016). This second objective had the purpose of filling the gap in the psittacine enrichment literature and identifying potential techniques to improve the well-being of captive kea. Two protocols were designed: one

based on the most common enrichment type from the parrot literature to determine its well-being efficacy on a novel species and one based on the least frequent enrichment type according to the results of the kea survey (Objective 1) to determine if such enrichment is validly under-utilised.

***Objective 3: Determine if captive kea contrafreeload***

Section 1.3.6 introduced the concept of contrafreeloading and discussed it as an indicator of how animals are motivated to perform specific behaviours to obtain resources. Research has been conducted to determine if some captive animals contrafreeload, arguing that contrafreeloading species should be able to display behaviours to obtain resources or their well-being could be compromised. Even with this discussion of contrafreeloading as a likely indicator of behavioural needs (e.g. Millar, 2013; Clark, 2013), some studies assume contrafreeloading is a behaviour common to all species and do not specifically test their study species for contrafreeloading behaviour in the absence of prior research (e.g. dolphins (*Tursiops truncatus*) in Clark, 2013). Contrafreeloading research is limited, with only one study overtly assessing the performance of contrafreeloading by a parrot species finding that subjects did contrafreeload (*P. erithacus* in van Zeeland et al., 2010). This thesis includes an experiment to determine if captive kea contrafreeload with the intention of determining if they require opportunities to express certain behaviours in captivity.

***Objective 4: Investigate captive kea's choices as a precursor for preference and motivation-based well-being***

Section 1.2.2 introduced the concept of preferences and motivation and their impact on well-being. This theory comes from the premise that animals make choices and decisions in their best interest and they suffer if they are not provided with stimuli that they are motivated to obtain (Mendl, 2001). This objective had the purpose of obtaining preliminary data on preferred task characteristics. For this, two experiments were designed.

The first experiment was designed as a follow-up from the foraging manipulation to determine if kea contrafreeloaded (Objective 3). Briefly, kea's preferences towards interacting with different manipulanda during a foraging task were investigated to discover which manipulanda were preferred by analysing subjects' choice sequence. Knowing kea's manipulandum preferences will be useful when designing tasks or enrichment opportunities to maximise engagement and increase the probability of displaying positive behaviours (e.g. contrafreeloading-related behaviours).

The second experiment involved a recent well-being perspective: the provision of appropriate challenges (Meehan and Mench, 2007). Briefly, this theory proposed that there

is a current focus on ensuring “the physical expression of feeding behaviours” but, actually, animals need to be challenged in “complex problem solving behaviours” (Meehan and Mench, 2007). Based on the framework of cognitive enrichment, and because most studies rely on tasks with a physical component (e.g. pressing buttons), the second experiment provided captive kea a cognitive task with no physical component, whose difficulty was quantified as a proxy to measure challenge level. Two modalities of the task varying in challenge level (i.e. difficulty) were simultaneously available to determine if kea showed a preference for either type.

## 1.9 Thesis structure

Chapter 2 describes the design and implementation of an online survey and its distribution among international kea holders to gain knowledge on the global status quo of kea captivity. It provides a descriptive account of kea demographics, common management protocols and the occurrence of abnormal behaviours in the captive kea population. The environmental and management variables surveyed are included in a regression analysis to predict if the occurrence of behavioural variables correlates with these variables.

Chapters 3 and 4 describe two different protocols that were implemented as putative enrichment opportunities. Using species-specific ethograms, the behavioural effects of these protocols are quantified and used to determine effects on kea well-being.

The protocol described in Chapter 3 consists of visual and auditory stimuli, which were identified in Chapter 2 as non-recurrent protocols. Briefly, these stimuli were played to kea and their general behaviour was measured during playback sessions and compared to a baseline phase (no stimuli being delivered) to determine if subjects’ activity budgets were modified (e.g. less abnormal behaviours, see Section 1.2.1 “Function approach”; more natural behaviours, see Section 1.2.3).

Chapter 4 consists of a food presentation manipulation. Briefly, this technique involved providing the subjects’ routine feedings in either a free-to-access condition or a work-to-access condition to determine if kea performed contrafreeloading behaviour, which has been signalled as an indicator of motivation towards exploration opportunities (see Section 1.3.6) and also to determine if it could induce positive changes in foraging behaviour (in accordance to the natural-living well-being framework).

The experiment presented in Chapter 5 appeared as a follow-up to Chapter 4. Several task-related variables (type of manipulation, access to food and food visibility) were used to determine which stimuli and conditions were preferred by kea.

Chapter 6 presents another study based on the feelings approach but this time a novel cognitive task was designed and implemented, following the novel “cognitive enrichment” category (see Section 1.6.2). This task consisted of visually discriminating a positive image; a successful discrimination led to a food reward, while failing to discriminate led to no reward. The difficulty of each modality was quantified, and these difficulties were used to identify and provide a task with low difficulty and a task with high difficulty to determine if kea showed a preference for either.

Finally, Chapter 7 includes an overall discussion on the findings of this thesis, also highlighting the general research shortcomings and the strengths of experimental chapters. It concludes with suggestions for future research that builds upon this body of work.

# Chapter 2. Survey of captive kea management as an evaluation of recommended practices

## Abstract

Suboptimal captive environments can negatively impact captive animal behaviour and well-being. To prevent these adverse effects, animals under human care should be managed to cater for their needs and promote their well-being. The New Zealand kea is a parrot species common in European zoos but information on its husbandry and well-being is lacking. There are guidelines that provide recommendations on their captive management and husbandry, but these are not science-based. Furthermore, there are no scientific studies assessing the well-being of captive kea. Here, the husbandry and enrichment protocols for captive kea were surveyed worldwide. An online survey was distributed to institutions listed as kea holders, collecting data for 190 kea. The survey included items about respondents' identification, kea demographics, feeding and enrichment protocols, physical environment, and kea behaviour. Husbandry practices were similar across institutions and matched the recommendations of the husbandry manuals. Most kea were housed with at least one conspecific, fed twice per day, and provided with daily enrichment. The most frequent types of enrichment were food and activity-based opportunities. Behaviours correlated with poor well-being on psittacines were found to have varying occurrences: pacing (17%), feather-damaging behaviour (2.5%) and, abnormal reproduction (11%). The proportion of feather-damaging kea per enclosure was found to be predicted by a linear regression model ($F(7, 46)=2.655$, $p=0.022$), with feeding frequency being a significant predictor ($p=0.001$). This correlation was discussed as possibly being a countermeasure for pre-existing feather damaging behaviour. This study signals how the behaviour-based well-being of captive kea may be compromised in captivity, with little evidence of environmental factors correlating with abnormal behaviours.

## 2.1 Introduction

Entertainment, education, and conservation are the main purposes for keeping wild animals in zoos and aquaria and there are several management tools in place to aid the captive breeding and conservation of certain species. Taxon Advisory Groups (TAGs) create Regional Collection Plans (RCPs) that recommend species to be kept in captivity and how to manage them. European Endangered Species Programmes (EEPs) and European Studbooks (ESBs) are two management levels that obtain information about all animals of a given captive species and plan for its management. Other mechanisms are also available in different regions and at various levels (e.g. Species Survival Plans (SSPs), Animal Care Manuals (ACMs), Scientific Advisory Groups (SAGs)).

As discussed in Chapter 1.4, parrots are commonly kept in zoos. “Parrots are one of the most threatened bird orders with 28% of species (ca. 360) listed as globally threatened and 56% of species in decline”, (European Association of Zoos and Aquaria, 2019). Captive breeding programmes in zoos have assisted in the conservation of threatened and endangered parrot species (e.g. *Cyanopsitta spixii* (Bampi and Da-Ré, 1994), *Neophema chrysogaster* (Smales et al., 2000), *Strigops habroptilus* (Elliot et al., 2001)). Table 2.1 presents a list of parrot species currently managed by a Zoo and Aquaria Association[8] (American: AZA, European: EAZA, Australasia: ZAA). The main objective of these programmes is to control and optimise the captive breeding of wildlife with a focus on health, mortality, reproductive output, genetic compatibility, and animal movements.

One of the outputs of these management programmes are husbandry guidelines that derive from “current science, practice and technology of animal management to maximise capacity for excellence in animal care and welfare” (AZA, 2019). The contents of these documents follow a template provided by the head organisation. For example, AZA Animal Care Manuals include information on taxonomy, ambient and social environments, containment, transport, nutrition, veterinary care, reproduction, behaviour management, and research (AZA, 2019). Similarly, EAZA Guidelines include details on biology and field data, enclosure, feeding, social structure, breeding, behavioural enrichment, handling, and veterinary care (EAZA, 2019). Table 2.2 shows a list of the available manuals and guidelines for parrot species.

[8] Associations of Zoos and Aquaria are membership-based organisations whose mission is to facilitate cooperation within the animal-keeping community and ensure institutions possess the highest standards of animal care and breeding. Several associations exist in different geographical locations (e.g. Europe, America, Britain and Ireland, Australasia). Animal-keeping centres are not required to be a member of an association.

Table 2.1 – List of parrot species currently managed by an AZA, EAZA or ZAA programme and their conservation status. Data from: AZA, 2019; EAZA, 2019 and Zoo Aquarium Association Australasia, 2019.

| Species | IUCN Status | Programmes |
|---|---|---|
| *Cacatua haematuropygia* | Critically Endangered, population decreasing | EEP |
| *Cacatua moluccensis* | Vulnerable, population decreasing | EEP |
| *Cacatua sulphurea citrinocristata* | Critically Endangered, population decreasing | EEP |
| *Probosciger aterrimus* | Least Concern, population decreasing | EEP, SSP, AZA Studbook |
| *Lorius domicellus* | Endangered, population decreasing | ESB |
| *Lorius garrulous* | Vulnerable, population decreasing | ESB |
| *Nestor notabilis* | Endangered, population decreasing | ESB, SSP, AZA Studbook, ZAA |
| *Amazona brasiliensis* | Near-threatened, population increasing | EEP |
| *Amazona autumnalis lilacina* | Endangered, population decreasing | EEP, Best Practice Guidelines |
| *Amazona viridigenalis* | Endangered, population decreasing | EEP |
| *Anodorhynchus hyacinthinus* | Vulnerable, population decreasing | EEP, SSP, AZA Studbook |
| *Ara ambiguus* | Endangered, population decreasing | EEP, AZA Studbook |
| *Ara glaucogularis* | Critically endangered, population stable | EEP, SSP, AZA Studbook |
| *Ara militaris* | Vulnerable, population decreasing | ESB |
| *Ara rubrogenys* | Critically endangered, population decreasing | EEP, SSP, AZA Studbook |
| *Guaruba guarouba* | Vulnerable, population decreasing | ESB, SSP, AZA Studbook |
| *Pyrrhura cruentata* | Vulnerable, decreasing | ESB |
| *Cyanopsitta spixii* | Critically endangered, population unknown | Studbook, Special Conservation Programme |
| *Neophema chrysogaster* | Critically Endangered, population decreasing | Studbook |
| *Strigops habroptilus* | Critically endangered, population increasing | Studbook |
| *Rhynchopsitta terrisi* | Endangered, population decreasing | Studbook |
| *Deroptyus accipitrinus* | Least concern, population decreasing | SSP |
| *Rhynchopsitta pachyrhyncha* | Endangered, population decreasing | SSP, AZA Studbook |
| *Nestor meridionalis* | Endangered, population decreasing | Managed by Zoo Aquarium Association Australasia |
| *Cyanoramphus unicolor* | Vulnerable, population stable | Managed by Zoo Aquarium Association Australasia |

Table 2.2 – List of parrot species for which management and/or husbandry resources exist. Data from: AZA, 2019; EAZA, 2019, Zoo Aquarium Association Australasia, 2019 and Australasian Zoo Keeping, 2011.

| Species | Resource | Association |
|---|---|---|
| Parrots | Parrot supplement to the Bird demonstration guidelines | EAZA |
| *Amazona lilacina* | Best practice guidelines | EAZA |
| *Amazona rhodocorytha* | Husbandry manual | AZA |
| *Amazona versicolor* | Husbandry manual | Forestry Department of Saint Lucia |
| *Amazona versicolor* | Management guidelines | Jersey Wildlife Preservation Trust |
| *Rhynchopsitta pachyrhyncha* | Husbandry manual | AZA |
| *Rhynchopsitta pachyrhyncha* | Management guidelines | Jersey Wildlife Preservation Trust |
| *Cyclopsitticini spp.* | Husbandry manual (draft) | Undisclosed |
| *Nestor notabilis* | Husbandry manual (draft) | ZAA |
| *Nestor notabilis* | Captive Management Plan and Husbandry Manual | Department of Conservation, New Zealand |
| *Ara ararauna* | Husbandry manual | Western Sydney Institute of TAFE, Richmond College |
| *Ara ambiguus* | Management guidelines | EAZA |
| *Anodorhynchus hyacinthinus* | Husbandry manual (draft) | EAZA |
| *Polytelis swainsonii* | Husbandry manual | Western Sydney Institute of TAFE, Richmond College |
| *Neophema chrysogaste* | Husbandry manual (draft) | Undisclosed |
| *Polytelis alexandrae* | Husbandry guidelines | Western Sydney Institute of TAFE, Richmond College |
| *Glossopsitta concinna* | Husbandry guidelines | Western Sydney Institute of TAFE, Richmond College |
| *Cacatua spp.* | Husbandry guidelines | EEP |
| *Calyptorhynchus banksii* | Husbandry guidelines | Western Sydney Institute of TAFE, Richmond College |
| *Calyptorhynchus funereus* | Husbandry manual | Western Sydney Institute of TAFE, Richmond College |
| *Probosciger aterrimus* | Husbandry manual | EAZA |
| *Eolophus roseicapillus* | Husbandry guidelines | Western Sydney Institute of TAFE, Richmond College |

There is a mismatch between the species in Tables 2.1 and 2.2. This contrast is even larger when comparing the number of species in these tables with the number of species reported to be kept in captivity (232 as reported by Lindholm, 1999 but probably an under-representation due to its geographic and historic constraints). Ideally, there should be management guidelines for every species kept in captivity to promote their well-being but, given the lack of resources (e.g. scientific data, human resources, time) and conservation pressures (e.g. endangered vs. least-concern species), certain species are prioritised.

Kea are currently listed as Endangered by the IUCN Red List, with a decreasing population of 4,000 mature individuals reported in the wild (BirdLife International, 2017). An SSP is currently in place to manage the kea captive population (Pullar, 1996) and a dedicated Captive Management Program and a Husbandry Manual exist for captive kea (Table 2.2). The Husbandry Manual specifies the minimum housing requirements to keep kea in captivity (Pullar, 1996). The manual mentions how some captive kea (from the New Zealand population) are kept in conditions considered “substandard” but does not describe these conditions. The Husbandry Manual includes recommendations such as enclosure measurements, materials, furniture, social environment, diet, and breeding practices. While these recommendations are provided by aviculture experts, who are a valuable source of information given their practical experience, they are not completely based on scientific evidence.

The husbandry and management of captive kea has not been investigated beyond the recommendations from these resources. Chapter 1.5.1 discussed the few published studies discussing management of captive kea, including information on their reproductive output. For example, Woolcock (2000) discussed the diet, enclosure design, substrate, nesting sites, and furniture provided to captive kea, commenting that “the size of the enclosure is less critical than ensuring that it contains a variety of items to stimulate the Keas”, suggesting that enclosure complexity is a relevant factor for kea well-being (in-line with the recommendations of the Husbandry Manual) but without presenting supporting evidence.

A more recent kea manual in draft form (Orr-Walker, 2010) expanded on the management recommendations, including some references to the well-being literature. The manual introduced enrichment recommendations to satisfy the species’ behavioural needs (see Chapter 1.3.4) and positively impact kea well-being. It included a scientific rationale for enrichment recommendations based on stereotypies as behavioural indicators of parrot well-being (see Chapters 1.2.1.2 and 1.6.1.1). However, the manual only included one reference that discussed stereotypies and husbandry of captive kea. This report (Orr-Walker, 2005)

was an undergraduate project investigating correlations between management practices and the behavioural repertoire of a subset of the captive kea population in New Zealand. Via written surveys sent to kea holders, Orr-Walker (2005) calculated that 61% of the surveyed population (N=43) performed stereotypies and thus had a compromised well-being. There are no published studies on the expression of abnormal behaviours by captive kea or on the behavioural effects of different husbandry and enrichment practices, but abnormal behaviours have been reported and discussed in other parrot species (see Chapter 1.6.1). Anecdotal observations, both from the researcher and zookeepers, suggest that kea perform stereotypical behaviours.

Environmental enrichment opportunities for captive parrots, as explained in Chapter 1.6.2, frequently rely on the enrichment definition referring to environmental modifications that aim to positively impact the well-being of captive animals (Newberry, 1995). Briefly, parrot enrichment has been shown in particular to: increase foraging times (e.g. van Zeeland et al., 2013), improve feather condition (e.g. Lumeij and Hommers, 2008), promote egg laying (Millam, 1994) and minimise the occurrence of stereotypies (e.g. Meehan et al., 2004). Orr-Walker (2010) only suggested that kea should be enriched based on a high-frequency and high-novelty programme, assuming this protocol should yield optimal well-being.

Chapter 1.5.3 predicted the possible impact on kea well-being based on the parrot literature, observations from the researcher on a limited number of captive kea and the behaviours of kea in the wild. Following these research gaps, the objectives of this study are: 1) to determine what are the current management protocols for captive kea around the world, 2) to determine the occurrence of abnormal behaviours (recognised in captive parrots) in the captive kea population, and 3) to determine if the recommendations from the husbandry manual have an impact on said occurrence.

## 2.2 Materials and methods

### 2.2.1 Data collection

An online survey was created on the BOS© platform (University of Bristol, 2016). It included 18 questions regarding respondent information (institution, job title, seniority), kea demographics (number of male/female, juvenile/adult kea kept; juvenile classification was based on physical characteristics such as yellow ceres and eye rings, see Diamond and Bond, 1999), enclosure characteristics (trees, bushes, single rocks, rock formations, still water, running water, natural perches, artificial perches, nests, toys, ropes, cement, grass, bark, soil, mesh, glass, wood), species housed, indoor/outdoor, and if it was a walk-through exhibit), general husbandry and enrichment (feeding frequency, enrichment frequency,

enrichment types provided, enrichment examples) and kea behaviour (see Appendix 1 for a copy of the questionnaire). Enrichment types were surveyed as: foraging (defined as husbandry protocols designed to affect feeding strategies), sensory enrichment (defined as the provision of stimuli expected to engage or target a specific sense), social (defined as changes in social composition of the group or animal-human interactions), physical (defined as changes in furniture or objects available in the enclosure), or occupational (defined as tasks, problems or challenges).

The question on negative behaviours asked to report how many kea performed: pacing (defined as moving in constant, fixed patterns), feather damaging (defined as removing or damaging feathers from self) and abnormal reproductive behaviour (defined as: attempts at breeding with non-mates (Becky Muir, pers. comm.), early/late breeding (i.e. out of season), or non-breeding (i.e. breeding pairs not mating)). To minimise the negative connotation of the questionnaire and prevent respondents from not disclosing information on their stock (Katie Major, pers. comm.), kea caretakers were asked if kea displayed social play, tool use and "hanging by the beak from roof or branches" (this last behaviour was included based on casual observations of kea behaviour in captivity (see also Diamond and Bond, 1999) to balance the number of negative and positive questions.

Initially, zoos listed as kea holders (data provided by the European studbook coordinator, Nigel Simpson) were contacted by email or online form depending on the information available on their websites. If reached by a generic e-mail, zoos were asked to circulate the survey to the bird department. Kea management coordinators in America, Australasia and Europe also helped with survey distribution in their corresponding regions. Institutions that did not reply or answer the survey were later reached via their social media and given a second and final reminder. The survey was made available from September 2015 until February 2016. Zoos' identifiers were anonymised while summarising and analysing data.

When filling out a survey, respondents were asked to complete the questionnaire for one kea enclosure. The last question asked if there were more kea housed in other enclosures: if the respondent selected "No", the survey ended; if the respondent selected "Yes", a new questionnaire (with identical questions) was displayed to be completed for another enclosure. This system repeated until the respondent selected "No" in the last question. For cases where multiple enclosures were reported, only data from one were used for inferential statistics (enclosure was randomly chosen via coin toss (if two enclosures) or die toss (if more than two enclosures)).

One of the limitations of surveys and questionnaires as research tools is their validity and reliability. Appleton (2006) provided a framework that discusses how to determine validity and reliability. She first discussed validity based on “truth value” and “applicability”, indicating that a research instrument is valid when it measures what it intends to measure and that the results should be applicable to other areas or contexts. She then discussed reliability based on consistency, repeatability, and replicability of the data as well as “neutrality” or the lack of bias in the methods. To ensure the validity and reliability of the questionnaire, the researcher selected a location-based convenience sample of six zoos (seven kea enclosures) to visit. With these visits, the researcher intended to determine the level of agreement between questionnaire data from zoo staff and data obtained from his in-person observations. The researcher was based in the UK therefore all kea-keeping UK zoos were visited. Furthermore, the researcher was able to visit kea-keeping zoos in Nuremberg, Germany; Zürich, Switzerland; and Vienna, Austria. Zoos were told in advance about the visit. During visits, the researcher had a blank copy of the questionnaire and completed it based on his own observations of the kea, their enclosure, and their management. Statistical tests with these two data sets (direct observation data and keeper responses) would serve as an indicator of validity. This questionnaire is considered reliable as it included all kea-keeping institutions and surveyed both normal and abnormal behaviours, thus minimising bias effects due to just surveying either type. Also, the use of an online survey facilitates the repeatability of the experiment.

### 2.2.2 Data analysis

Survey responses recorded in BOS© were logged into Excel to obtain descriptive statistics. Six independent variables were created with the survey data. Habitat (i.e. enclosure) diversity (HD) was calculated based on the elements and furniture found inside an enclosure; it had a minimum value of zero if the enclosure did not include any of the surveyed elements and a maximum value of nineteen if the enclosure contained all surveyed elements. If an enclosure only included some elements, an intermediate value was totalled by adding the elements described by the survey respondent (e.g. an enclosure containing trees, running water and rocks would receive a HD score of 3). Feeding frequency (FF) was calculated with the answers to the corresponding questions; if kea were fed once per day, FF would have a value of 1, if twice a value of 2, and so on. Enrichment frequency (EF) was calculated with the answers of the corresponding question; EF had a value of zero if no enrichment was provided, one if it was delivered on a monthly basis, two if delivered on a weekly basis or three provided on a daily basis. Enrichment diversity (ED) was calculated based on the types of enrichment provided. ED had a value of zero if no enrichment was

provided, 1 if only one type was provided, 2 if two types were provided, and so on. A binomial variable (multiple species - MS) indicated if the enclosure housed only kea or kea and other species. Another binomial variable (walk-through - WT) indicated if the enclosure allowed for the public to walk through it or not. A continuous variable, NK, represented the number of kea housed in an enclosure. Behavioural data were logged as the proportion of birds in each enclosure described to perform said behaviour.

Surveys completed by the researcher during zoo visits were logged into Excel. Cochen's κ test was used to compare the agreement between survey responses from zoo staff to data from zoo visits. Two separate agreement analyses were performed. The first analysis compared data on: elements inside the enclosure, materials out of which the enclosure was made of, substrate; enclosure type (indoor/outdoor, walk-through) and species housed (single or multi-species). The second analysis compared surveyed and observed behaviours. All data were coded as presence/absence for agreement analysis. The reason of performing two separate tests is that the researcher was able to accurately evaluate the physical environment in each zoo visit by just ticking the elements and species observed in the enclosure. The researcher had limited time during the visit to perform behavioural observations (see Chapter 2.2.1) and obtaining an accurate representation on behaviour and management (e.g. feeding and enrichment frequencies) would not be possible[9]. One zoo kept kea in two enclosures; these two data sets lacked independence but they were both included in reliability tests as the purpose of these was just to calculate reliability and not to perform inferential statistics with these on the dependent variables. Altman's (1999) guidelines were used to determine agreement levels between survey and zoo-visits data.

Prior to inferential statistics, data from six zoos were revised as they reported more than one kea enclosure (i.e. non-independent data points). Data from only one enclosure of these zoos were randomly kept via coin flip for the five zoos reporting two enclosures each and via a rolled die for the zoo reporting five enclosures. Inferential statistics were then performed on independent data points, which totalled 150 kea in 54 enclosures. Linear multiple regressions were performed using HD, ED, EF, MS, WT, NK as predictor variables for each of the behaviours' proportion in an enclosure. Statistical significance was determined according to $p<0.05$ unless stated otherwise.

[9] For example, to accurately report on observed enrichment frequency, the researcher would have to observe the kea for one month to be able to classify enrichment provision as daily, weekly, monthly, or non-existent.

## 2.3 Results

### 2.3.1 Demographics

Survey data were obtained for 190 kea, representing 77% of the captive population reported in 2015. These were housed in 65 enclosures across 55 zoos (80% of worldwide zoos reported to keep this species). Survey responses referred to 121 European kea, 34 American (United States and Canada), 31 from New Zealand and four from Asia (Figure 2.1). The age-sex ratios of the surveyed kea were: 43% adult males, 35% adult females, 14% juvenile males and 7% juvenile females, totalling 149 adults and 41 juveniles.

### 2.3.2 Husbandry and enrichment

The largest kea group housed in a single enclosure was formed by twelve individuals and occurred in one zoo. The second and third largest flocks included eight and seven kea. Seven zoos kept singly housed kea. The most recurring housing condition was keeping kea as pairs, happening in 33 enclosures from which 25 were adult male-female pairs. Only males were found to be kept as same-sex groups in five enclosures. Most kea were kept in the presence of only conspecifics, but ten enclosures contained kea and other bird species. Five enclosures were described as indoor enclosures, 37 as outdoor and 24 had both an indoor and outdoor area. Five enclosures allowed for the public to walk through them.

The feeding routine was surveyed in terms of feedings per day with the most common frequency being twice (54%), followed by once (24%) and three times (9%). Eight kea enclosures were fed on a more frequent schedule, ranging from two or three main feedings with additional feeding sessions up to six times per day. Provision of enrichment opportunities was surveyed as daily, weekly, monthly, or non-existent. Most enclosures were provided with daily (50%) or weekly (34%) enrichment. A monthly frequency was found in eight enclosures (12%). From all responses, ten were found to include in their enrichment rota all five types of environmental enrichment opportunities surveyed, 25 enclosures received four enrichment types, 21 three types, eight received two types and only one enclosure received one enrichment type. The enrichment category most utilized by zoos was foraging enrichment (92%), followed by physical (89%), occupational (75%), social (63%) and sensory (32%). The most recurring examples of enrichment were toys and natural items (e.g. browse; mentioned 23 times), puzzle feeders and boxes (19 responses), scatter feeding (13) and food inside cages (10) or bags (6). Less common examples were kabobs, frozen treats, and floating food with four mentions each. Some zoos reported different husbandry and enrichment for some of their enclosures as their kea took part of free-flying shows or demonstrations; these kea received more frequent feedings.

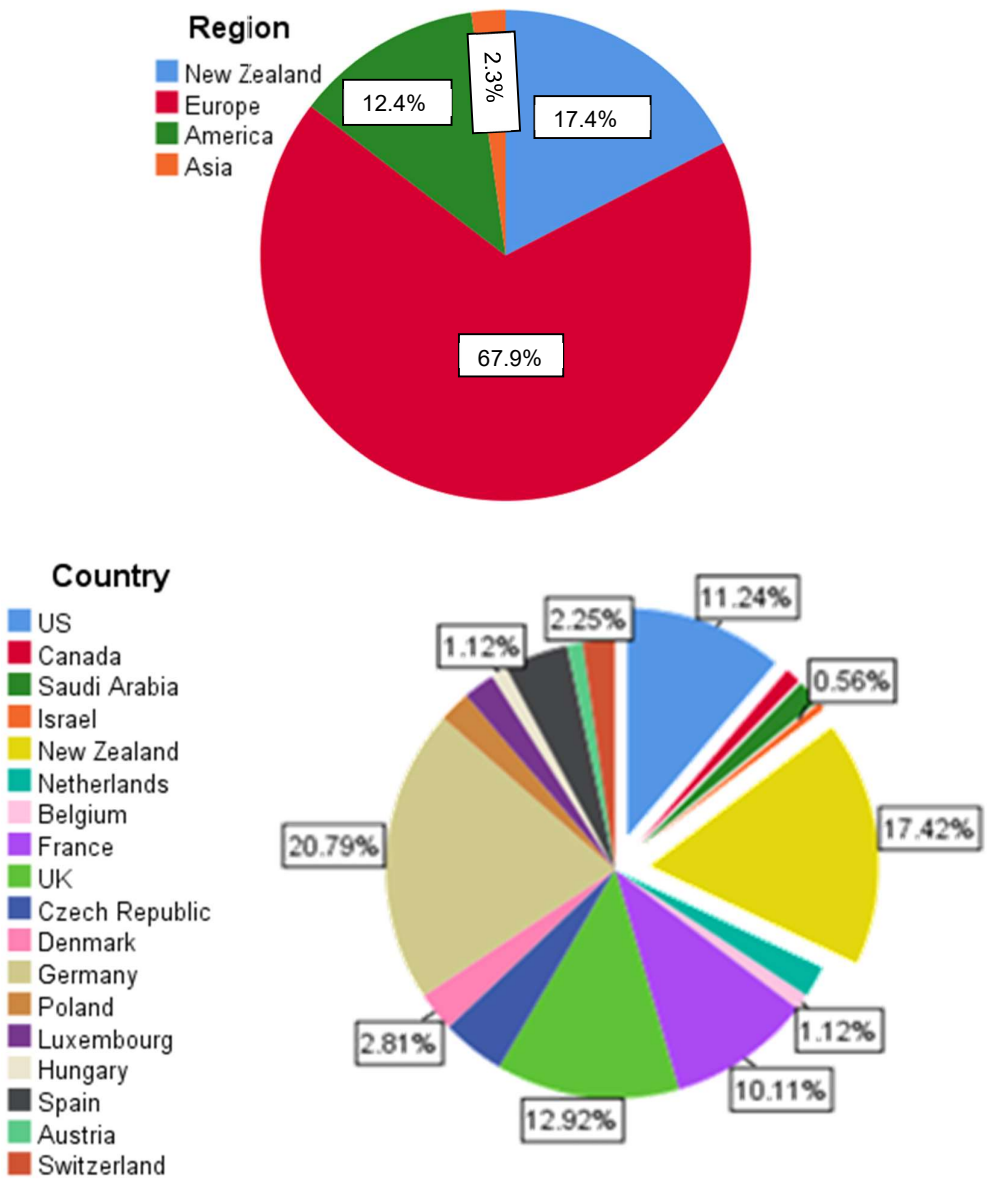



Figure 2.1 – Distribution of surveyed kea. Top: regional distribution of surveyed kea. Bottom: country distribution of surveyed kea. Most captive kea were in Europe (top figure), with Germany being the country housing the most birds (bottom figure).

### 2.3.3 Reported behaviour occurrence

Stereotypical locomotion in the form of pacing had a reported occurrence of 17% (34 kea) in the surveyed kea population. From these, 70% were males and 5% juveniles. Feather damaging behaviour was reported for five adult birds (2.5%): one male and four females. Abnormal reproduction was reported in 22 cases (11% of surveyed individuals), including 12 males and 10 females. No juveniles were reported to engage in feather-damaging behaviours or to display abnormal reproduction.

More than half of the surveyed kea (67%) were reported to engage in social play. This behaviour was similarly distributed between males (61 kea) and females (54 kea). A higher proportion of juveniles were reported to play (68%) compared to adults (58%). A total of 84 parrots were reported as tool users. This behaviour was performed in similar proportions by males (43%) and females (46%). Tool use appeared more widespread among adult (46%) than juvenile (37%) kea.

### 2.3.4 Reliability analysis

The first reliability analysis (Table 2.3) showed that there was significant agreement ranging from moderate to very good when comparing physical environment data from survey responses and direct zoo observations. The second reliability analysis (Table 2.4) showed that the agreement of behaviour data from surveys and zoo visits ranged from poor to very good. Only two datasets showed significant (very good) agreement. Two datasets did not include variation in the zoo visit data (i.e. no behaviours were observed) and Cochen's κ was not calculated, as variation in the dataset is a requirement. Instead, a descriptive measure is provided in terms of the percentage of behaviours showing agreement between survey data and zoo visits. The remaining four datasets did not show significant differences.

Table 2.3 – Cochen's κ statistical parameters. Compared data included presence/absence of elements inside the enclosure. Standard error represents κ's standard deviation.

| Survey | κ | Agreement strength | p | Std. Error |
|---|---|---|---|---|
| Blackpool Zoo | 0.611 | Good | 0.004 | 0.172 |
| Bristol Zoo enclosure 1 | 0.542 | Moderate | 0.011 | 0.202 |
| Bristol Zoo enclosure 2 | 0.908 | Very good | <0.001 | 0.090 |
| Birdworld Farnham | 0.538 | Moderate | 0.011 | 0.181 |
| Heidelberg Zoo | 0.553 | Moderate | 0.007 | 0.170 |
| Munich Zoo | 0.431 | Moderate | 0.029 | 0.182 |
| Vienna Zoo | 0.468 | Moderate | 0.019 | 0.174 |
| Walter Zoo | 0.596 | Moderate | 0.002 | 0.167 |

Table 2.4 – Cochen's κ statistical parameters. Compared data included presence/absence of pacing, feather damage, social play, and tool use. Standard error represents κ's standard deviation. *The researcher did not detect any of the surveyed behaviours and the statistical test could not be performed; percentages indicate how many behaviours showed agreement between survey and zoo-visit data.

| Survey | κ | Agreement strength | p-value | Std. Error |
|---|---|---|---|---|
| Blackpool Zoo | 1.000 | Very good | 0.025 | 0.000 |
| Bristol Zoo enclosure 1 | 1.000 | Very good | 0.025 | 0.000 |
| Bristol Zoo enclosure 2 | 0.545 | Moderate | 0.171 | 0.362 |
| Birdworld Farnham | 60% agreement* | | | |
| Heidelberg Zoo | 80% agreement* | | | |
| Munich Zoo | 0.167 | Poor | 0.709 | 0.446 |
| Vienna Zoo | 0.429 | Moderate | 0.171 | 0.379 |
| Walter Zoo | 0.615 | Good | 0.136 | 0.318 |

### 2.3.5 Husbandry factors and behaviour prediction (enclosure level)

Data from one survey response (14 kea in two enclosures) were not included in regression analyses because answers from kea demographics and number of kea performing the surveyed behaviours did not match. Data from a second respondent (24 kea in three enclosures) were not included in regression analyses because the kea had been recently relocated into newly built enclosures and it was not known if data corresponded to previous or current enclosures. Zoos with multiple kea enclosures were inspected and only one enclosure was kept for statistical tests (chosen randomly as previously described).

Survey data used for inferential statistics totalled 54 enclosures and 150 kea. Pacing was reported to occur in 20 (37%) enclosures. Feather damaging was reported in five (9%) enclosures. Social play was reported in 33 (61%) enclosures. Tool use was reported in 32 (59%) enclosures. Habitat diversity (HD) had a mean of 9.2 with a range of [4, 13] (Figure 2.1). Enrichment frequency (EF) had a median of 1 with a range of [1, 3] (Figure 2.2). Enrichment diversity (ED) had a median of 4 with a range [1, 4] (Figure 2.3). Number of kea in an enclosure (NK) had a mean of 2.8 with a range of [1, 12] (Figure 2.4). There were only 3 (5%) walk-through and six (11%) multi-species enclosures.

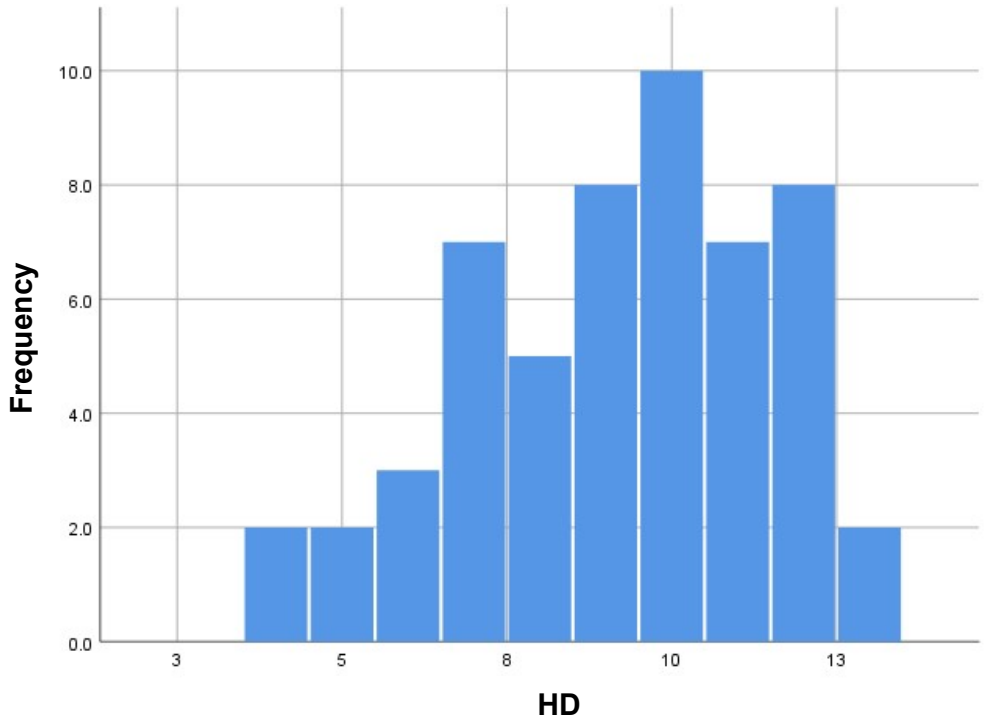



Figure 2.2 – Habitat diversity (HD) histogram showing the frequency of surveyed kea enclosures in each HD rating. HD was calculated by adding up all the elements reported inside the enclosure.

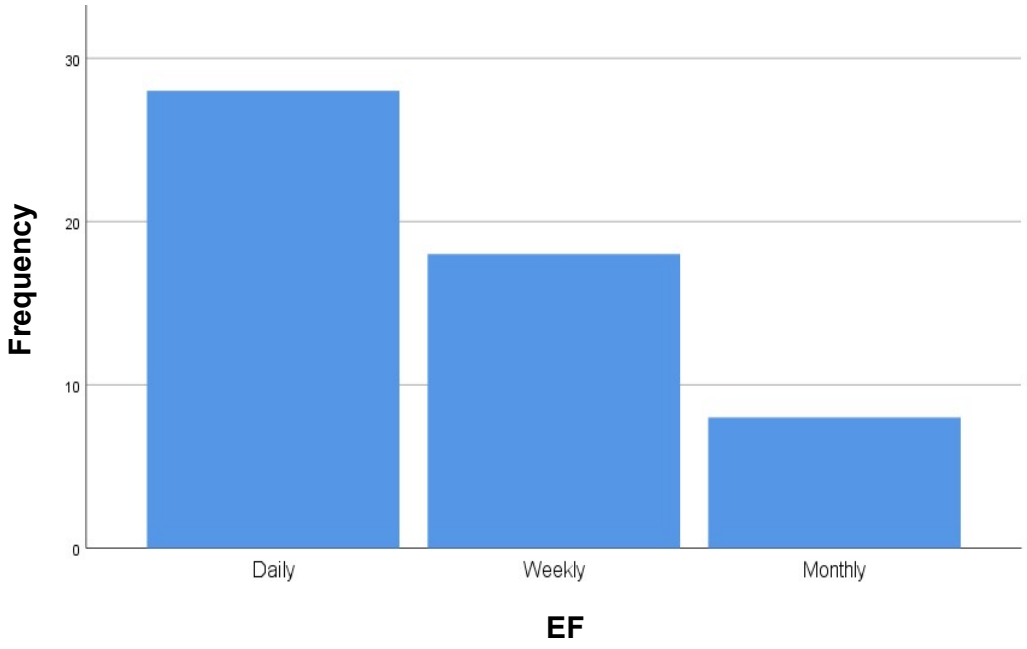



Figure 2.3 – Enrichment frequency (EF) histogram showing the frequency of surveyed kea enclosures reported in each of the three enrichment frequency categories (daily, weekly, or monthly).

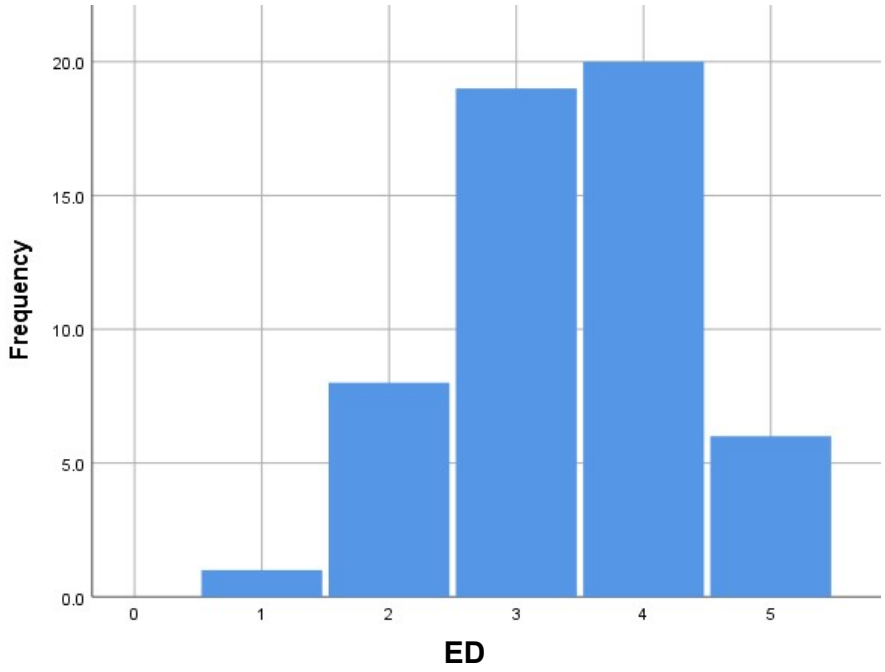



Figure 2.4 – Enrichment diversity (ED) histogram showing the number of surveyed kea enclosures providing one or more types of enrichment (types of enrichment surveyed were: foraging, physical, social, occupational, and sensory).

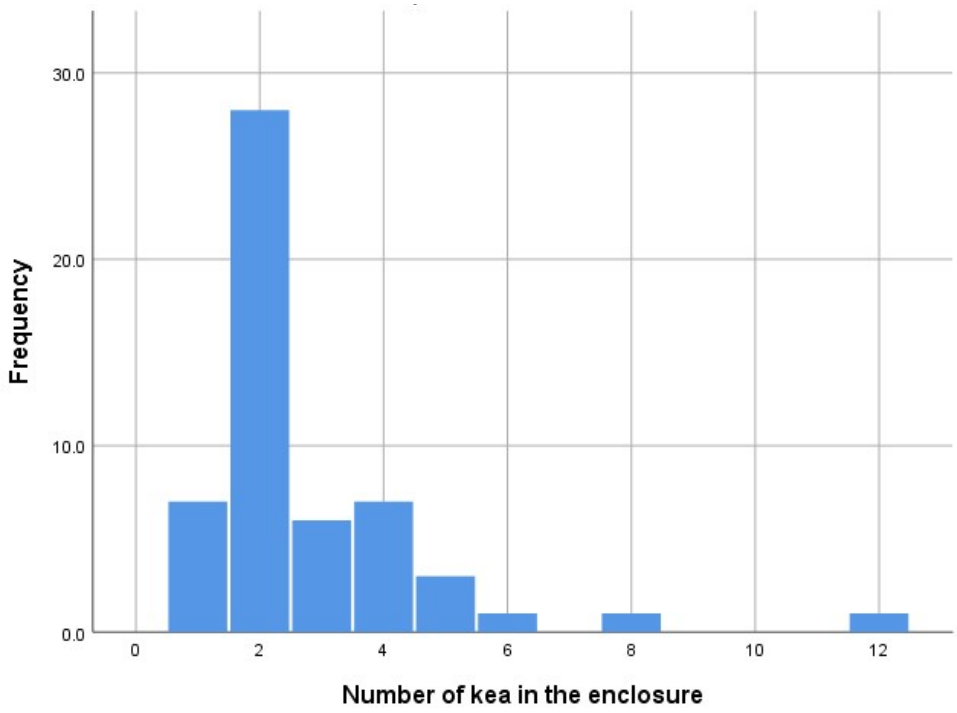



Figure 2.5 – Number of kea (NK) histogram showing the frequency of surveyed enclosures housing different numbers of kea.

### 2.3.5.1 Linear multiple regressions using behaviour proportions

A multiple regression was run to predict the proportion of pacing kea per enclosure by HD, FF, EF, ED, NK, WT, and MS. The adjusted $R^2$ (measure of the proportion of the variance in pacing explained by the model) in this model is 7.5%. There was no statistically significant prediction of pacing proportion by the predicting variables $F(7, 46)=1.613$[10], $p=0.156$. None of the variables significantly affected the prediction ($p>0.05$) (Table 2.5).

A multiple regression was run to predict the proportion of feather damaging kea per enclosure from environmental diversity, feeding frequency, enrichment frequency, enrichment types, number of kea in the enclosure, type of enclosure (walk-through and mixed species). The adjusted $R^2$ in this model is 17.9%. There was a statistically significant prediction of feather damaging proportion by the predicting variables $F(7, 46)=2.655$, $p=0.022$. Only Feeding Frequency significantly affected the prediction ($p=0.001$) (Table 2.6).

Table 2.5 – Regression analysis for the proportion of kea per enclosure showing pacing behaviour. For all variables $p>0.05$.

| Variable | Unstandardised coefficient | Coefficient standard error | Standardised coefficient |
|---|---|---|---|
| Constant | 0.102 | 0.326 | |
| HD | 0.027 | 0.025 | 0.163 |
| EF | -0.099 | 0.078 | -0.193 |
| ED | -0.004 | 0.063 | -0.010 |
| NK | -0.027 | 0.030 | -0.135 |
| WT | 0.314 | 0.233 | 0.192 |
| MS | 0.016 | 0.177 | 0.014 |
| FF | 0.057 | 0.049 | 0.166 |

Table 2.6 – Regression analysis for the proportion of kea per enclosure showing feather damaging behaviour. **p=0.001, otherwise $p>0.05$.

| Variable | Unstandardised coefficient | Coefficient standard error | Standardised coefficient |
|---|---|---|---|
| Constant | 0.024 | 0.173 | |
| HD | -0.003 | 0.013 | -0.036 |
| EF | -0.014 | 0.041 | -0.047 |
| ED | -0.012 | 0.033 | -0.054 |
| NK | -0.025 | 0.016 | -2.223 |
| WT | -0.173 | 0.124 | -0.188 |
| MS | 0.101 | 0.094 | 0.150 |
| FF | 0.094** | 0.026 | 0.485 |

[10] This and following regression parameters formatted according to APA guidelines.

A multiple regression was run to predict the proportion of kea with abnormal reproduction per enclosure from environmental diversity, feeding frequency, enrichment frequency, enrichment types, number of kea in the enclosure, type of enclosure (walk-through and mixed species). The adjusted $R^2$ in this model is 0.3%. There was no statistically significant prediction of abnormal reproduction proportion by the predicting variables $F(7, 46)=1.020$, $p=0.430$. Only type of enclosure (walk-through) significantly affected the prediction ($p=0.038$) (Table 2.7).

Table 2.7 – Regression analysis for the proportion of kea per enclosure showing abnormal reproduction. *Indicates $p=0.038$, otherwise $p>0.05$.

| Variable | Unstandardised coefficient | Coefficient standard error | Standardised coefficient |
|---|---|---|---|
| Constant | 0.275 | 0.286 | |
| HD | 0.004 | 0.022 | 0.028 |
| EF | 0.047 | 0.068 | 0.108 |
| ED | -0.047 | 0.055 | -0.138 |
| NK | -0.009 | 0.026 | -0.053 |
| WT | 0.436* | 0.205 | 0.316 |
| MS | -0.063 | 0.155 | -0.063 |
| FF | -0.034 | 0.043 | -0.116 |

A multiple regression was run to predict the proportion of kea showing social play per enclosure from environmental diversity, feeding frequency, enrichment frequency, enrichment types, number of kea in the enclosure, type of enclosure (walk-through and mixed species). The adjusted $R^2$ in this model is 3.7%. There was no statistically significant prediction of social play proportion by the predicting variables $F(7, 46)=1.294$, $p=0.275$. None of the variables significantly affected the prediction ($p>0.05$) (Table 2.8).

Table 2.8 – Regression analysis for the proportion of kea per enclosure reported to showing social play. For all variables $p>0.05$.

| Variable | Unstandardised coefficient | Coefficient standard error | Standardised coefficient |
|---|---|---|---|
| Constant | -0.200 | 0.418 | |
| HD | 0.059 | 0.032 | 0.289 |
| EF | 0.112 | 0.100 | 0.173 |
| ED | 0.056 | 0.080 | 0.112 |
| NK | 0.003 | 0.038 | 0.011 |
| WT | 0.101 | 0.299 | 0.049 |
| MS | -0.098 | 0.226 | -0.065 |
| FF | -0.073 | 0.062 | -0.168 |

A multiple regression was run to predict the proportion of kea showing tool use per enclosure from environmental diversity, feeding frequency, enrichment frequency, enrichment types, number of kea in the enclosure, type of enclosure (walk-through and mixed species). The adjusted $R^2$ in this model is -3.9%. There was no statistically significant prediction of tool use proportion by the predicting variables $F(7, 46)=0.714$, $p=0.660$. None of the variables significantly affected the prediction ($p>0.05$) (Table 2.9).

Table 2.9 – Regression analysis for the proportion of kea per enclosure reported to show tool use. For all variables $p>0.05$.

| Variable | Unstandardised coefficient | Coefficient standard error | Standardised coefficient |
|---|---|---|---|
| Constant | -0.031 | 0.421 | |
| HD | 0.056 | 0.032 | 0.283 |
| EF | 0.081 | 0.100 | 0.129 |
| ED | -0.031 | 0.081 | -0.064 |
| NK | -0.037 | 0.038 | -0.151 |
| WT | -0.350 | 0.301 | -0.176 |
| MS | 0.190 | 0.228 | 0.131 |
| FF | 0.045 | 0.063 | 0.108 |

## 2.4 Discussion

The purpose of this study was to gather information on the current management of captive kea with a focus on their physical environment and environmental enrichment. The husbandry of captive kea was found to correspond with what the husbandry manuals recommend, as most kea were housed in enclosures with high environmental diversity, daily provision of different enrichment opportunities and in the company of conspecifics. Three abnormal behaviours identified from the parrot well-being literature (see Chapter 1.6.1) were surveyed to determine their occurrence in the captive population. Pacing behaviour had the highest occurrence, followed by and abnormal reproduction and feather damaging behaviour. Behaviours associated with good well-being were also reported to be displayed by captive kea. Inferential statistics were performed to determine if there were any correlations between management data and behaviour occurrence: only feather damaging behaviour was found to be predicted by husbandry parameters.

### 2.4.1 Online survey as a data collection method

In this study, the use of an online survey allowed to obtain specific information on kea husbandry with a high response rate. It is advised that when surveying a population, a representative, random sample should be chosen (Thwaites Bee and Murdoch-Eaton, 2016).

In this study, it was possible to send surveys to all registered kea-holders worldwide and data were obtained for the majority of these, thus eliminating the need of having to work with a data subset. It is necessary to acknowledge that this might be an under-representation of the actual number of kea in captivity, as there are private breeders, homeowners with pet kea (the researcher was aware of one kea kept as a pet) and zoos not affiliated to any zoological associations that do not report their stock.

Surveyed kea-holders had to answer at least 18 questions. There is no “golden rule” determining the number of questions (or pages) representing short or long questionnaires; considering a survey long or short may be a personal interpretation. Research on surveys as data-collection methods has shown contradicting results when comparing questionnaire length and return rate. These studies assessing questionnaire efficacy are a few decades old and focus on paper-based surveys (as online tools were not available or widespread), usually sent and returned via post. Berdie (1973) performed analysed the return rate of 1, 2 or 4-page questionnaires, finding no significant differences between return rate and these lengths. It is possible that the length contrast between each questionnaire was not large enough (i.e. there may not be much difference in answering one or two pages). Contrarily, Champion and Sear (1969) determined that longer questionnaires tended to be returned more frequently than shorter ones. Research has shown that online surveys show a trend towards higher and faster return rates (Lonsdale et al., 2006, but see Pan (2010) for a brief discussion on low response rates in some cases). In this study, the survey was sent and received electronically, which explains the high response rate as there was no need to post it back. Pan (2010) also hypothesised that lifestyles could have a negative impact on return rate, given the limited attention span for tasks outside of someone’s work and hectic daily schedules. Following the hypothesis that longer questionnaires result in low return rates, the survey in this study could have been reduced to increase return rate but this could result in losing important data.

### 2.4.2 Findings on captive conditions (descriptive level)

Survey data showed that the management of captive kea is in accordance with the recommendations of the Husbandry Manual. The social environment of captive kea coincides with the recommendation of keeping more than one bird. However, seven kea were reported to be housed singly. Parrots are considered as “exceptionally social birds” (Engebretson, 2006) with kea not being an exception, as they live as family groups and aggregate as bigger clusters to engage in foraging and/or social play behaviours (Diamond and Bond, 1991). The lack of an appropriate social context in captivity has been suggested to negatively affect psittacine physical and behavioural well-being (Graham, 1998; Meehan

et al., 2003), thus suggesting that singly housed kea may have poor well-being. Survey data indicated that ten kea enclosures were multi-species exhibits (details about the other species housed were not surveyed but anecdotal observations by the researcher found three European enclosures in which kea were kept with other parrots such as macaws and cockatoos; see also Woolcock, 2000). Most studies on this topic only explore the effects on activity-budgets, with no discussion on animal well-being (*e.g.* Pearson et al., 2010; Mallavarpu et al., 2011; Buchanan-Smith et al., 2013; Valuska et al., 2013). The ten enclosures in which kea were kept with other species require further research into their well-being implications.

Six enclosures allowed the public to walk inside them. Walk-through enclosures have the potential to positively impact zoo visitors' experience and reactions (Luebke and Matiasek, 2013) but their effect on animal well-being has not been determined. Walk-through enclosures allow for human-animal interactions (HAI) to occur (these can also occur between animals and their caretakers). Martin and Melfi (2016) defined HAI as the initiation of a behaviour by an animal or a human directed towards the other. They also described how HAIs can evolve into HARs (human-animal relationships) based on the human or animal being able to predict the other's behaviour and modify their own as a response. Claxton (2011) commented that zoo visitors are rarely familiar to zoo animals and thus do not form relationships with them. However, there is still an effect due to zoo visitors in the behaviour and well-being of captive animals. For example, a study on quokkas (*Setonix brachyurus*; Learmonth et al., 2018) found that animals were more fearful when humans were inside the enclosure compared to when the enclosure remained closed to the public. Cotton-topped tamarins (*Saguinus oedipus*), Diana monkeys (*Cercopithecus Diana*) and ringtailed lemurs (*Lemur catta*) were found to be negatively affected by the presence of visitors as evidenced by increased agonistic behaviours and decreased inactivity (Chamove et al., 1988). Mitchell et al. (1991) also found that higher visitor attendance negatively impacted the well-being of mangabeys (*Cercocebus chrysogaster*), measured by increased aggression. However, other studies showed that zoo visitors may elicit positive responses on captive animals. Jones and colleagues (2016) found that the well-being of lemurs (*Eulemur coronatus*) was not compromised by visitors entering the enclosure. Interestingly, Jones and colleagues (2016) interpreted the higher frequency of lemur-visitor interactions over an extended period as a sign of habituation or even enrichment. Captive otters (*Aeonyx cinerea*) showed more play and feeding behaviours when visitors were present, described as a positive effect on their well-being (Owen, 2004). The conflicting effects of zoo visitors on animal well-being complicates the discussion of walk-through exhibits and their effect on kea well-being. Another element in the inter-specific social context of captive animals is

“stockmanship” or the “management of animals by someone who does this in a safe, effective and low-stress manner (Ward and Melfi, 2015). Rough handling of livestock has shown to increase their fear responses (pigs in Pedersen et al., 2003; cows in Breuer et al., 2000). On the other hand, positive HARs can be considered as enrichment opportunities if they encourage positive behaviour responses (Claxton, 2011). Unfortunately, this study did not investigate the role of the zookeeper and their relationships with the kea and their well-being.

Twenty-four percent of surveyed enclosures were fed once per day (less than what the Husbandry Manual recommends), which may suggest a well-being compromise based on research on other captive parrots showing that increasing foraging time reduces inactivity and encourages a naturalistic activity budget (Rozek et al., 2010). In terms of enrichment, most kea enclosures (86%) received three or more enrichment types but only half of the enclosures received enrichment daily. Enrichment diversity and frequency have been shown to positively impact animal well-being. Dogs exposed to a low-frequency enrichment protocol had poorer well-being compared to dogs in a high-frequency protocol, as observed by increased cortisol levels in the former group (Lefebvre et al., 2009, but see Chapter 1.2.4 for the relevance of cortisol as a well-being indicator). Enrichment diversity for laboratory rats had a positive impact on their well-being by promoting species-specific behaviours (Abou-Ismail, 2011). Foraging and physical enrichment were the most reported types in the survey. These results match the findings of Rodríguez-López (2016), describing how parrot enrichment studies have focused on physical and foraging opportunities. Sensory enrichment was the least frequent type according to the survey.

### 2.4.3 Findings on reported behaviours (descriptive level)

Data showed that abnormal behaviours recognised in other parrot species occur in the captive kea population. Feather damaging behaviour had a low occurrence, described in only five individuals. Upon inspection of the kea engaging in this behaviour, there was indication that females are more susceptible to this problem. Psittacine research on feather damaging behaviour has also found a similar sex factor (van Zeeland et al., 2009). Given the low occurrence of feather damage, it does not appear to be a generalised problem within the captive population. However, the welfare of the five feather-damaging kea should be further inspected to determine if the origin of the problem is behavioural or medical.

Abnormal reproduction (e.g. non-breeding), had a moderate occurrence. This behaviour is a probable consequence of captivity, since in most cases kea pairs are formed instead of allowing mate-choice, which may explain cases of incompatibility. Mating attempts with non-mate birds could be explained by frustrated behavioural needs, also a result of

captive management. In the wild, kea start breeding from the age of three (females) or four years (males; Diamond and Bond, 1999). Wild kea have been reported to have a low-frequency breeding. In one location, only 20% of adult males were observed feeding fledglings, an indication of low nest productivity (Bond and Diamond, 1999). Female kea may spend several years building and defending a nest, which adds to the low productivity (Bond and Diamond, 1992). These characteristics may explain the cases of abnormal reproduction in captivity. For example, captive kea are often provided a “ready-made” nest box and they are expected to utilise it, which does not allow for total control over nest building.

Pacing was the abnormal behaviour with the highest occurrence, reported in 17% of the surveyed kea and it was performed mostly by males. There are no published studies quantifying the occurrence of stereotypical locomotion on kea. However, the literature recognises stereotypies as a problem in parrots (Engebretson, 2006). There is an unpublished undergraduate report on the captive kea population in New Zealand (70 individuals in 27 facilities) that found an occurrence of 61% for stereotypical behaviours (which included head-swinging, route pacing, self-feather plucking and aggression) also via surveys (Orr-Walker, 2005). Unfortunately, the report grouped all stereotypical behaviours, which does not allow a comparison with the pacing data from this study. Orr-Walker (2005) mentions more male kea showing stereotypies (65% of the stereotyping kea were males), which agrees with the results from this study (70% of the pacing kea were males).

There is no evidence on other parrot species that explains this sex-difference in stereotypical behaviour; research on other taxa has found contrasting results. Nagy-Reis et al. (2019), for example, discovered that subadult, male capuchins (*Sapajus* spp) performed more pacing behaviour than all sex-age categories in their study (adults, juveniles, and infants). This difference was explained based on distal (evolutionary pressure for wild male capuchins to leave their natal groups resulting in increased (and thwarted) locomotor behaviour in captivity) and proximal (stress caused by the captive social context) causations. In the wild, male and female kea abandon their parents and nesting site (Diamond and Bond, 1999) which does not explain the sex-based difference in pacing in this study. A problem with Nagy-Reis and colleagues’ methods is that they only differentiated males from females in the adult and sub-adult categories (and their sample did not include any sub-adult females). Authors failed to recognise this limitation but they did mention that sub-adult males may be more susceptible to pacing on the basis of group-dispersal and associated stress as sub-adult females usually stay in their natal group (Nagy-Reis et al., 2019). Other species showed a different effect of sex on pacing behaviour (e.g. female captive mink paced more than males, Mason, 1993) or no effect at all (e.g. no sex differences in stereotypy levels of captive brown bears, Montaudouin and Le Pape, 2005). Pacing in kea has been suggested

to be a dominance display by males (Raoul Schwing, pers. comm.) which fits with the male-female ratio of pacing kea in this study but this result warrants further research.

Social play and tool use had a high occurrence in the captive population, which could indicate optimal well-being based on natural behaviour (see Chapter 1.2.3). In the wild, kea have been reported to partake in intensive, complex play sessions (Diamond and Bond, 1991; Diamond et al., 2006) often relying on vocalisations that can act as a trigger for aerial, object or social play (Schwing et al., 2017). There are no published studies on the effects on captive kea play behaviour factors but research on other taxa has shown that a more complex environment increased social play (humans in Barbour, 1999; domestic pigs in Chaloupkova et al., 2007). Play behaviour has been considered as an indicator of optimal well-beinh (Held and Spinka, 2011; Ahloy-Dallaire et al., 2018) based on the idea that if animals' essential needs are satisfied, they can use their "free time" for "leisure activities" (e.g. play). Survey data showed that 67% of the kea engaged in social play, thus these kea should not have poor well-being. On the other hand, the 33% not reported to engage in social play could have poor well-being. Fraser and Duncan (1998) discussed how play behaviour is performed when animals' needs are satisfied. It is possible that the environment of non-playing kea did not provide the necessary stimuli to either satisfy their needs or to promote play behaviour. Another explanation for this result could be related to kea's age. Social play has been discussed to be a characteristic of juvenile animals (Diamond and Bond, 2004). This survey found that adult kea conform 79% of the surveyed sample. Following Diamond and Bond's (2004) premise, adult kea should play less and account for the 33% of non-playing birds. Social play in wild kea has been described as "much more broadly distributed among age groups" (Diamond and Bond, 2004). In this study, play was surveyed as social play, which, by definition, requires a social context. Survey data indicated that this may be the limiting factor as kea reported to engage in social play were more frequently kept in larger groups. Based on the data of the present study, the social context is believed to be the limiting factor as the remaining predicting variables (enrichment types and frequency, feeding frequency, enclosure diversity, walk-through and multi-species) included both playing and non-playing kea across their different levels.

Half of the adult kea and one-third of the juveniles were described as tool users. Wild kea are not considered natural tool users (Auersperg et al., 2010) but laboratory experiments with captive specimens have shown that kea are able to solve a second-order tool use task (Auersperg et al., 2010), use tools with flexibility (Auersperg et al, 2011b), navigate a tool end (Auersperg et al., 2011a), and rely on social information in a tool use task (Gajdon et al., 2011). Defining tool use "is problematic, often arbitrary or subjective, sometimes anthropocentric, and open to interpretation" (Bentley-Condit and Smith, 2010). Attempts at

defining this behaviour range from “use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal” (van-Lawick-Goodall, 1970) to “the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool” (Beck, 1980). Reaching a goal seems to be the common element in tool-use definitions and thus it cannot be ensured if the kea described as tool users were employing an object to reach an objective.

### 2.4.4 Reliability analysis

The reliability analysis for the physical environment showed that the eight zoo responses significantly agreed with direct observations, suggesting that there is moderate to very good precision in the whole dataset for the physical environment. However, the reliability analysis also showed that behavioural data for one enclosure had poor reliability with the researcher’s observed behaviours. The seven remaining comparisons ranged from moderate to very good reliability (albeit only two with significance). These results could be interpreted as an indication that 12.5% of the behavioural responses were not accurate. An explanation for this discrepancy is the duration of the behavioural observations during zoo visits. The researcher was able to directly observe kea in their enclosure for 30 min, recording the behaviour of all individuals. This duration may not be sufficient to obtain an accurate representation of captive kea behaviour and thus the lack of reliability may be due to the researcher’s limited observations rather than erroneous survey data. Even with a conservative approach, having 88.5% of the data correctly describing surveyed behaviours is not detrimental to this study thanks to the considerable number of survey responses received.

### 2.4.5 Effects of captive conditions on behaviour

The proportion of feather-damaging kea per enclosure was the only variable significantly predicted by a linear regression model with Feeding Frequency being the only significant predictor (with a positive relationship). This result does not indicate that high feeding frequencies cause feather-damaging behaviour, but that the predictor correlates with the behaviour.

Research on feather damaging behaviour in chickens has been shown to be “strongly associated with the performance of foraging behaviour […] and is considered […] to be re-directed foraging behavior” (Meehan et al., 2003). For example, feather pecking behaviour by laying hen (*Gallus gallus domesticus*) chicks was reduced and prevented by

providing a foraging substrate to increase foraging behaviours, whereas providing sand to promote bathing behaviour had no effect on feather pecking (Huber-Eicher and Wechsler, 1997; see also Nicol et al., 2001). The literature on captive parrot behaviour recognised the influence of foraging opportunities on feather damaging behaviour. When juvenile Amazon parrots (*Amazona amazonica*) were offered opportunities designed to increase the work required to forage (i.e. foraging duration), feather picking behaviour decreased (on subjects already performing this behaviour) and was prevented from developing (when compared to subjects not expose to this foraging opportunities; Meehan et al., 2003). However, the study offered physical structures as enrichment in conjunction with foraging opportunities, thus restricting any conclusions being made specifically for foraging manipulations.

It is possible that the relationship between feeding frequency and feather damaging is different to what was predicted: kea that exhibit feather damaging behaviour may receive increased foraging opportunities to alleviate this problem. Whilst this hypothesis is plausible, two other variables would have been expected to appear as significant predictors: enrichment frequency (EF) and enrichment diversity (ED), following recommendations to minimise feather damaging behaviour (e.g. Chitty, 2003b). The literature on psittacine feather-damaging behaviour has identified influencing factors or components, such as: genetic, social, physical, neurobiological, medical, behavioural and environmental (e.g. van Zeeland et al., 2009; van Zeeland and Schoemaker, 2014). This survey only investigated housing and management conditions, so it is possible that other variables played a more key role in the development of feather damaging behaviour.

A more plausible explanation lies in the fact that feather-damaging behaviour had a low occurrence, with only five enclosures reported to house feather-damaging kea. These low frequencies resulted in larger effects solely due to sample size (i.e. 100% of feather-damaging kea were fed more than once per day). Feather-damaging behaviour needs to be further investigated to determine if its aetiology matches that of other psittacines.

### 2.4.6 Final remarks

In this study, environmental diversity was defined based on the number of different elements inside an enclosure. Environment complexity is defined in the literature in terms of enclosure size and the number of available features and items. For example, Kitchen and Martin (1996) and Scott and LaDue (2019) described enclosures housing marmosets (*Callithrix jacchus jacchus*) and elephants (*Loxodonta africana*), respectively, as small simple (i.e. non-furnished), small complex (i.e. furnished) and large complex (i.e. furnished) enclosures. Other studies have taken the “enclosure quality” approach by only varying the available items in an enclosure. Studies on lobsters (*Homarus americanus*; Cenni et al.,

2010) and rats (Abou-Ismail et al., 2010) defined complexity based on the availability of physical elements vs. enclosures lacking them. Studies often report environmental complexity together with enclosure size without controlling for either factor (e.g. Estep et al., 1978; Jensvold et al., 2001; Liu et al., 2003). Valuska and Mench (2013) determined that larger enclosures reduced aggressive behaviour in rabbits. Onagers (*Equus hemionus onager*) transferred from large to small enclosures saw an increase in cortisol, considered as a negative well-being effect as it was comparable to the stress effect from proximity to human activities (Vick et al., 2011 but see Chapter 1.2.4). Enclosure size was also shown to be positively correlated with distance travelled and negatively correlated with pacing behaviour in captive tigers (*Panthera tigris*; Breton and Barrot, 2014). Scott and LaDue (2019) determined that enclosure complexity (based on the number of physical features) correlated with higher activity levels and enclosure size affected the incidence of stereotypic behaviour in a study on two elephants (*Loxodonta africana*). These results were also reported by Kitchen and Martin (1996) in laboratory-housed marmosets (*Callithrix jacchus jacchus*), as subjects showed increased activity levels in large and more complex cages, with stereotypical behaviours only being performed in small cages.

Based on these findings, it is possible that not only environmental diversity but also enclosure size play affects the behaviour of captive kea, with a potential impact on pacing behaviour. Enclosure size was not assessed in this study as the researcher was previously informed by two zoos that they did not have enclosure measurements in their records. The researcher was encouraged by one zoo to measure the enclosure himself (but not all zoos allowed non-staff to go inside the enclosure). Asking for enclosure measurements in the survey could have deterred respondents to complete it if they had to obtain the measurements themselves. Nonetheless, obtaining data on enclosure size would be important to re-test the validity of the predictive models presented here.

A total of 83.3% of the respondent zoos were members of a regional zoological association (e.g. EAZA, AZA). Therefore, surveyed zoos are biased towards institutions with “the highest standards of care and breeding” (EAZA, 2019) which may affect the occurrence of both positive and negative behaviours. A total of 37.5% of the surveyed zoos who were not members of a Zoological Association reported the occurrence of negative behaviours, against 48.9% of member zoos. While there were less non-member zoos (8) than member zoos (47), data showed that abnormal behaviours occur in both types of zoos. Also, this study was able to contact all kea holders listed on the ZIM’s Species Holding Report with a response rate of 78.5%, which shows that even with a sample biased towards accredited zoos, it is representative of the captive kea population.

This study managed to collect information on 77% of the captive kea population officially reported during the year in which the experiment was conducted, which is a notable highlight. This turnaround exceeds that of other studies surveying captive wildlife in a global scale (e.g. Rowden and Rose, 2016). Getting data on the management of these many captive kea is useful for animal caretakers, as they can see if their husbandry practices are on par with those of other institutions. Also relevant is the information on specific enrichment examples. Providing enrichment opportunities is not straightforward (hence the objectives of this thesis) but having a list of enrichment items or tasks that have worked with the species is always useful.

A weakness of this study is the lack of definitions for the three behaviours not associated with negative well-being. “Hanging by the beak from roof / branches” was believed to be self-explanatory. It was included in the survey based on casual observations of captive kea and to balance the number of questions associated and not associated with negative well-being. This behaviour was not included in statistical analysis. A common definition of tool-use is the modification of the shape, position or condition of an object or organism via an instrument or object held or carried by the subject (Beck, 1980; Seed and Byrne, 2010). For a kea to be considered a tool-user, it should be seen using an object to alter another object, a conspecific or itself. It is possible that survey respondents misinterpreted object play or object manipulation (behaviours frequently seen in captive kea) as tool-use instances. A comparable situation occurs with social play. Defining this behaviour is not simple, given the subjectivity of play itself. Instances of play behaviour were assumed to be evident, especially given the complex play behaviours kea exhibit in the wild (Diamond and Bond, 1999). While, convenience visits and reliability analyses attempted to measure the agreement between reported and observed behaviours, showing positive results, the behavioural component of this study should be considered of a stepping-stone towards determining putative indicators of well-being in captive kea.

## 2.5 Conclusions

- Data on husbandry and enrichment practices for 190 kea in 65 enclosures across 55 zoos were collected by means of an online survey.

- Captive conditions appeared congruent with the recommendations of the husbandry manuals: most enclosures housed a kea pair in outdoor settings. Two feedings per day and daily provisions of enrichment of the foraging and physical categories were the most frequent practices.

- A subset of seven surveyed institutions were visited to determine if survey responses were reliable, obtaining data for eight enclosures. Responses referring to the physical environment had moderate to very good reliability. Responses referring to kea behaviour had poor to very good reliability.

- The proportion of kea per enclosure showing feather-damaging was the only variable significantly predicted by a regression model, with foraging frequency being a significant predictor.

# Chapter 3. Sensory enrichment: behavioural responses during exposure to visual and auditory stimuli

## Abstract

Environmental enrichment involves the provision of certain stimuli or opportunities to captive animals with the objective of improving their well-being, with most efforts often attempting to either decrease behaviours associated with poor well-being or increase natural/species-specific behaviours. Early enrichment categorisations identified five non-exclusive types: social, occupational, physical, nutritional, and sensory. Research appears focused on assessing nutritional, physical, and occupational enrichment, with less attention given to sensory enrichment. Sensory enrichment relies on providing visual, auditory, tactile, and/or olfactory stimuli that can elicit intrinsic motivation (i.e. motivation not linked to obtaining or manipulating a reward). This study determined the enrichment potential of providing sensory stimuli in the form on naturalistic and non-naturalistic sounds and videos to captive kea based on behaviour observations. Preening ($X^2$=12.107, df=4, p=0.017), drinking ($X^2$=10.857, df=4, p=0.028), chewing wire ($X^2$=14.08, df=4, p=0.007, and object manipulation ($X^2$=9.658, df=4, p=0.047) behaviours showed significant differences across the different stimuli, with naturalistic videos showing higher behavioural durations. Additionally, pacing behaviour showed a non-significant decrease in performance when comparing baseline (i.e. no stimuli being delivered) to experimental phases. This study presented behavioural evidence supporting the provision of sensory stimuli to captive kea, highlighting the simplicity of its delivery, and suggesting its planned inclusion into enrichment programmes.

## 3.1 Introduction

Chapter 1.6.2 introduced environmental enrichment to improve the well-being of captive animals. Bloomsmith et al. (1991) categorised enrichment opportunities as social, physical, nutritional, occupational, and sensory based on the types of items, tasks or stimuli provided, with this classification being useful to identify resources and systematically analyse their effects. Sensory enrichment appears less prominent in the published literature. Searching on the Web of Science platform using “sensory” and “enrichment” as **topic** keywords yields 1278 results, adding “animal” as a third topic keyword reduced results to 248. Repeating this search using “sensory” and “enrichment” as **title** keywords yields 52 results, adding “animal” as a third title keyword reduced results to 12. The psittacine enrichment research focuses on physical, nutritional, or occupational opportunities (Rodríguez-López, 2016, Williams et al., 2017). The putative enrichment opportunities given to captive kea (Chapter 2) appear congruent with these biases; there are no studies investigating the well-being effect of sensory stimulation on captive kea and this enrichment type was reported to have a low occurrence in zoos (Chapter 2).

The lack of sensory enrichment research partly supports the need for studies assessing this type of enrichment. Additionally, identifying opportunities that stray away from external rewards (e.g. food and toys) is another relevant research avenue. Intrinsically motivated enrichment does not rely on the provision of external reinforcers or rewards to elicit behavioural responses (Tarou and Bashaw, 2007). Sensory enrichment could be classified as intrinsic given that behavioural responses to it are not linked to a reward (albeit see Section 3.4.2 for studies including toys during sensory enrichment protocols).

A problem with intrinsic motivation is that its associated behavioural effects are often short-lived in comparison to extrinsic motivation (Tarou and Bashaw, 2007). An explanation for this difference is based on habituation. Habituation occurs when animals’ responses to stimuli decrease over time (Murphy et al., 2003). Extrinsically motivated enrichment opportunities have a lower probability of triggering habituation and this has been previously proven (e.g. behavioural responses decreasing with repeatedly presented reinforcers, Skinner, 1932). Enrichment based on intrinsic motivation has shorter effects than extrinsic motivation (Tarou and Bashaw, 2007). Identifying enrichment opportunities that are intrinsically motivated and have low habituation should help with the management of captive animals as these opportunities: should require less resources (no rewards needed), could be provided for longer periods or multiple times (minimising caretaker efforts in finding and providing novel enrichment) and, potentially, have a positive impact on animal well-being.

This Chapter has the main objective of providing sensory stimulation to captive kea and determine its potential as intrinsically motivated enrichment. A review of previous enrichment studies is presented next as guidance to identify relevant stimuli and well-being indicators. This overview follows the categorisation of sensory enrichment of Bloomsmith et al. (1991) and Wells (2009) to systematically present studies.

### 3.1.1 Visual stimuli

Captive animals have been exposed to visual stimuli (e.g. photographs and videos) as part of the protocols of behavioural research (Wells, 2009) but few studies have explored their well-being impact. The interest in studying the relationship between visual stimuli and well-being was first expressed by Klüver (1933). He exposed several primate species to motion pictures and observed their responses. Results seemed contradicting, as one prosimian and one primate did not appear to attend to the stimuli whereas Cebus monkeys (*Sapajus* spp.) showed fear responses when presented videos depicting predators. The low sample size and descriptive nature of Klüver's (1933) work do not allow to draw general conclusions on sensory enrichment but the fear response showed a potential detrimental effect on well-being.

It was not until several decades later that studies began to measure the well-being effects of visual stimulation via indicators. Brent et al. (1989) found a decrease in stereotypies in 14 singly housed chimpanzees (*Pan troglodytes*) exposed to TV programmes. This behavioural effect was more profound when subjects were also given toys to manipulate. Platt and Novak (1997) performed a similar experiment on rhesus monkeys (*Macaca mulatta*), but now including singly and group-housed subjects. Monkeys were shown videos of familiar or nonfamiliar conspecifics and humans and were also allowed to manipulate a joystick to navigate a cursor in a video game system. When the cursor touched a specific location on the screen, a sound was played, and a food reward was dispensed. Exposure to stimuli increased activity levels and decreased social grooming in group-housed subjects (discussed to be indicators of good well-being, e.g. Broom, 1991). While Platt and Novak did not discuss assess their protocols in terms of well-being, they did conclude that protocols "may be appropriate means by which to promote well-being" based on a lack of habituation and attention to stimuli. However, the videogame confounded results based on foraging (food reward), physical (joystick manipulation) and auditory (beep sound) enrichment, not allowing to determine an effect only due to visual stimuli.

A more recent study on two cetacean species (*Tursiops truncatus* and *Steno bredanensis*, Winship and Eskelinen, 2018) presented cartoons, live-action cetaceans, or live-action films without cetaceans. Subjects were more attentive to the playback device

when it displayed videos compared to when it did not display anything, and males performed aggressive behaviours towards the playback device. Attentiveness and aggression were not significantly different across stimuli, thus suggesting no well-being relevance of these protocols, but only based on these two behaviours.

Keeling and Hurnik (1993) exposed 20 chickens (*Gallus gallus domesticus*) to four visual stimuli: a real cage placed next to the test cage, a video of a cage, a conspecific placed next to the test cage and a video of a conspecific. Foraging behaviour was measured in terms of food consumed, food pecks and amount of food per peck during exposure to stimuli. Data suggested that videos of conspecifics and real conspecifics served as "social facilitators" due to the increase in foraging behaviours during these treatments. This study did not evaluate protocols in the context of well-being but given the effects on foraging behaviour (often described as a normal behaviour associated with positive well-being, Broom, 1991), these stimuli could be enriching. Non-focal birds (those used in the real conspecific treatment) were food deprived for 24 hours to ensure that they foraged during tests; results being dependent to food-restrained birds limit the applicability of this study. For example, if a zoo wanted to modify the (foraging) behaviour of an animal, it would be unethical to food-deprive certain subjects to use them as "facilitators". Furthermore, the provision of conspecifics (social enrichment) confounds the analysis in terms of visual enrichment.

In another study, videos were presented to socially housed domestic chicks to determine positional preferences (Clarke and Jones, 2000). Chicks' responses were compared between baseline conditions (no stimuli) and: 1) moving or still images, 2) bright or dim images, 3) colour or black-and-white images, 4) complex or simple images, and 5) varying degrees of complexity. Simple images consisted of geometric shapes presented as screensavers, complex images were made of more than one simple shape, and complex stimuli were animated cartoons. For each comparison (1-5 above), chicks were found to spend more time closer to displays showing moving, bright, colour and complex images. These findings were loosely described in terms of well-being, suggesting that chicks were motivated to explore novel stimuli and enrichment opportunities should allow this exploration.

Coulon et al. (2014) conducted an experiment on visual enrichment that appropriately controlled for auditory and social confounders. Wild-caught and hand-reared starlings (*Sturnus vulgaris*) were individually housed and placed in an isolated, soundproof chamber to control for social interactions and sensory stimulation not coming from experimental cues. Fifteen starlings were presented muted videos of natural landscapes and eight starlings were shown a grey display for two non-consecutive hours per day for five successive days.

Abnormal behaviours (somersaulting, repetitive cage perching, head tilting, repetitive screen pouncing, repetitive pecking, and wing tremble) were recorded in the first and last experimental days. Abnormal behaviours developed in all subjects, attributed to a change in living quarters as they were previously housed as groups in bigger enclosures. Videos of landscapes were effective in modulating high rates of abnormal behaviours but were discussed to not be enriching as they did not prevent the development of abnormal behaviours.

Besides presenting images and videos, research has also relied on mirrors as visual stimuli. Parrott and colleagues (1988) studied the effect of temporarily isolating group-housed sheep in a room with mirrors finding that the availability of mirrors attracted subjects' attention and was correlated with lower cortisol levels, interpreted as a positive effect on well-being. McAfee et al. (2002) presented mirrors to six stabled horses, finding that exposure to mirrors resulted in a reduction of stereotypical behaviour and other "potentially undesired behaviours" such as head nodding and head threats. Mirrors were also provided to individually and group-housed rabbits (Dalle Zotte et al., 2009). Rabbits were described to prefer mirrors by eating and staying in the enclosure section containing them. While there were no well-being assessments, authors suggested that "mirrors offer some advantages, perhaps related to comfort and welfare". The potential of mirrors as social enhancers (i.e. creating the illusion of larger groups) is now recognised. Mirrors are common tools for the management of some species (see Whitfield, 2002). For example, mirrors have been shown to positively impact the well-being of captive flamingos (*Phoeniconais minor*) by promoting the performance of species-specific marching behaviour (thought to be associated with nesting and socialisation; Pickering and Duverge, 1992).

Enrichment based on visual stimuli appeared biased towards non-avian species with most interventions relying on videos displaying snatural and captive environments, conspecifics (self via mirrors), animated films, and shapes. Visual enrichment was often assessed via behavioural indicators, with most studies focusing on specific behaviours (e.g. attentiveness and abnormal behaviours) rather than taking a general approach.

### 3.1.2 Auditory stimuli

Research on the effects of exposure to music on human behaviour and mood has sparked interest in determining if there are similar effects on non-human subjects in the context of environmental enrichment (Wells, 2009) assuming that animals perceive and respond to said stimuli similarly to humans (Panksepp and Bernatzky, 2002). Alworth and Buerkle (2013) provided a review of studies utilising music as auditory stimulation for captive animals. Exposure to music affected learning and development by *enhancing* performance in

cognitive tasks (Rauscher et al., 1998; Wadhwa et al., 1999; Aoun et al., 2005; Kim et al., 2006; Xu et al., 2009; Chaudhury et al., 2010). However, there is indication that the effect on learning and memory is species and stimulus dependent (e.g. stump-tailed macaques (*Macaca arctoides*) performed *worse* in a delayed response task when listening to music than when listening to white noise (Carlson et al., 1997)).

Alworth and Buerkle (2013) commented on how music can be "pleasant" as it may activate specific regions of the human brain involved in "reward processing, motivation, emotion and arousal" (see Blood and Zatorre, 2011 for a detailed overview on what pleasant music entails, such as eliciting positive affective states or changes in neurological activity). Alworth and Buerkle (2013) did not find any studies on non-human animals discussing the perception of "pleasurable music" based on reward circuitry but they cited Panksepp and Bernatzky (2002) as an example of how dopamine levels in domestic chick brains increased upon exposure to music.

Stress responses (the actions of the 'classic' physiological stress systems: hypothalamic-pituitary-adrenal or sympathetic-adrenomedullary) have been common dependent variables in studies assessing the effects of music on animals. In one study, mice were exposed to one of four stimuli (march and serenade music and blue-filter and red-filter lighting) finding that serenade music correlated with "lower levels of adrenocorticotropic hormone and noradrenaline, indicative of decreased stress" (Hu et al., 2007). Another study found that exposure to music resulted in a reduction of the "suppressive effects of stress on immune parameters" on mice and an enhancement of the "immune parameters and the anti-tumour response" on rats injected with cancer cells (Núñez et al., 2002). While a very promising result, authors discussed how the different interactions at the molecular, cellular, and functional levels complicate a general conclusion. Also, contradicting data is presented by research on primates with *Chlorocebus aethiops* not showing significant differences in stress parameters (heart rate, blood pressure, respiratory rate, and body temperature) between subjects exposed to harp music or no music (Hinds et al., 2007).

Abnormal behaviours are also common dependent variables in music research, with studies showing conflicting results. Exposing rhesus monkeys (*M. mulatta*) to radio music reduced the performance of stereotypic behaviours (O'Neill, 1989). However, baboons (*Papio hamadryas Anubis*, Brent and Weaver, 1996) and prosimians (*Otolemur garnettii*, Hanbury et al., 2009) exposed to radio music did not show any behavioural differences (including stereotypies). Similar contradictions occur with bird species. For example, domestic chicks exposed to music and ambient sound levels performed fewer separation (i.e. stress) calls after being temporarily isolated from their social group compared to those

exposed to silence (Normansell, 1989; Panksepp and Bernatzky, 2002). In contrast, chickens with and without access to music displayed similar fear levels, assessed by tonic immobility[11] responses (Gross and Siegel, 1983). On the other hand, adult hens exposed to environmental noise and music showed longer tonic immobility durations than hens exposed to only environmental noise (Campo et al., 2005).

One study was found to provide auditory stimuli to captive parrots (Williams et al., 2017). Parrots were exposed to either no music, classical music, pop music, rainforest sounds, parrot vocalisations, or talking radio. Behavioural analyses determined that "calm vocalisations"[12] were not performed during exposure to pop music and talking radio, and preening behaviour increased overall. The absence of calm vocalisations was considered detrimental, but authors did not discuss why pop music or talking radio had a negative effect apart from suggesting that external cues elicited calm vocalisations, which were masked by these two stimuli. This study had several limiting factors that were discussed such as small sample size and short treatment durations (two days per auditory cue). However, authors failed to recognise "species" as a confounding factor. They tested macaws (genus *Ara* and *Anodorhynchus hyacinthinus*), one Amazon (*Amazona oratrix*) and African greys (*Psittacus erithacus*), which are described to have "broadly similar behaviour and ethological needs". These taxa are allopatric and differ in their wild ecology and behaviour (e.g. macaw species visiting mud cliffs as part of their foraging behaviour, *P. erithacus* making seasonal movements and being highly gregarious, BirdLife International, 2016; 2018) and thus the presented stimuli may be perceived differently (e.g. wild *P. erithacus* are not found in rainforests and thus these sounds could be irrelevant).

Auditory enrichment also appears biased towards mammalian species, with birds were mostly represented by poultry and one study on parrots. There is a larger variation in auditory stimuli provided to captive animals compared to visual stimuli, ranging from different music genres (classic, pop, "radio") to ambient noises and naturalistic sounds (e.g. rainforest sounds). The variables used to determine the efficacy of auditory cues as enrichment are also diverse, including performance in cognitive tests, physiological parameters, abnormal behaviours, and general activity budgets.

[11] Tonic immobility in chickens is defined as a reduction in responsiveness following physical restraint appearing to be homologous to a predatory episode (Boissy, 1995).
[12] Defined as "Individual expresses a species-typical sound associated with being calm. Calm vocalisations included contact calls, chucking, purring etc. and were low in volume, pitch and intensity and were often accompanied by other calm behaviours, maintenance behaviours or non-agonistic social encounters."

### 3.1.3 Other sensory stimuli

Research on olfaction, taste and touch is less extensive. Wells (2009) and Clark and King (2008) have reviewed olfactory enrichment classifying stimuli as species-specific (those odours that are ecologically relevant or specific to the subject species' natural habitat), non-species-specific, and pheromonal.

Rafacz and Santymire (2014) provide an example of species-specific olfactory enrichment. Two group-housed, captive African wild dogs (*Lycaon pictus*) were presented with faeces from competitor and prey species. Data analyses showed that odours increased activity levels and species-specific behaviours (affiliation and submission) compared to baseline phases (no odours presented). Faecal glucocorticoid metabolites were shown to vary between subjects and odour types in two directions: some stimuli correlated with an increase and some with a decrease of metabolites). While the low sample size and possible social effects due to subject interaction limit the conclusions, research on captive lions (*Panthera leo*) supported these results, as presenting species-specific scents also increased affiliation (Wells, 2009).

Clark and King (2008) identified recurrent examples of non-species specific stimuli: "food scent, essential oils, herbs and spices, faeces, urine, commercial lures, and artificial scents" and explained that they are chosen based on "assumed relevance to the test subject". For example, two tigers (*Panthera tigris sumatrae*) and four cheetahs (*Acinonyx jubatus jubatus*) were given a hay ball sprayed with either cinnamon or catnip (Damasceno et al., 2017). Subjects performed significantly fewer pacing behaviours in the cinnamon treatment than when no hay ball was present. While the hay ball allowed for physical interactions that confound results, the hay ball sprayed with catnip showed different results, showing the possible relevance of the type of scent used. In another study, vanilla, valerian, coconut, and ginger scents given to kennel dogs were found to correlate with a decrease in vocalisation and locomotion (Binks et al., 2018). These results were discussed in terms of well-being, with excessive vocalisations and locomotion described as stress indicators (e.g. Stephen and Ledger, 2005). Authors acknowledged concerns about the validity of these behaviours as well-being indicators (e.g. inactivity discussed as "not a simple indicator as it may indicate apathy, boredom or learned helplessness" rather than relaxation). Besides these differing results in terms of the behavioural impact of olfactory enrichment, some studies also indicated that providing odours as stimuli did not have any effects (e.g. Fay and Miller, 2015; Myles and Montrose, 2015; Baker et al., 2018).

Research on stimuli targeting taste or touch is scarce (these two senses are not discussed in Wells, 2009). A Web of Science search using "gustation" and "welfare" as

keywords showed no results. Replacing “gustation” with “taste” showed 38 results, but only one discussed taste in a behavioural context. In this study (Van den Bos, 2000) gave pet cats three foods: their regular food, more flavoured food, and less flavoured food. Results were not discussed in the context of well-being but their finding that cats performed more hedonistic behaviours (lick/sniff feeding bowl, lick self’s lips and groom self’s face) when given more flavoured food may indicate a putative positive well-being effect. Another study on four captive dolphins (*Tursiops truncatus*) gave isolated individuals two floating devices that contained either plain ice cubes or ice cubes made with a mackerel solution to determine if subjects could discriminate them (Bouchard et al., 2017). Only the two females were found to be consistent in significantly discriminating between devices based on mean interaction times (measured via biting, pushing, and throw-follow behaviour) but did not discuss results in terms of well-being. .

### 3.1.4 Research gaps and study objectives

The discussion above showed how providing captive animals with sensory stimulation may impact their well-being, with visual and auditory stimuli being more recurrent in experimental protocols. Most studies do not follow a systematic approach in terms of provided stimuli or well-being assessment, as these appear arbitrarily selected (e.g. providing a specific music genre or measuring a single behaviour). Williams and colleagues (2017) conducted the only study assessing sensory (auditory) enrichment on captive parrots, with inconclusive results in terms of well-being based on calm vocalisations and preening behaviour. There are no studies investigating the well-being effect of sensory stimulation on captive kea.

This Chapter has the objective of systematically providing sensory stimulation to captive kea to determine its enrichment potential. Only auditory and visual stimuli were provided since: 1) -touch- stimuli involve physical contact/manipulation, which would confound the results as physical enrichment; 2) -taste- stimuli could be confounded as nutritional enrichment; and 3) olfactory stimulation has been anecdotally shown to elicit no response in captive kea (Becky Muir, pers. comm.). Furthermore, wild kea value auditory stimuli as they rely on their vocal repertoire for communication and social cohesion (Schwing et al., 2012). Additionally, wild kea have been shown to display play behaviours when exposed to audio recordings of conspecifics’ play vocalisations (Schwing et al., 2017). Thus, kea play vocalisations were chosen as a type of sensory stimuli, expecting results comparable to Schwing and colleagues (2017). This stimulus classifies as naturalistic as it is relevant in the species’ wild environment (Wells, 2009). Chapter 2 showed how behaviours associated with poor well-being in captive parrots were displayed by captive kea. Since there

is evidence that non-naturalistic sounds positively impact well-being by reducing abnormal behaviours in other taxa (e.g. O'Neill, 1989; non-significant effect in Wells et al., 2006) and to expand upon the results of Williams et al. (2017), non-naturalistic sounds were chosen as a second modality. Additionally, given the knowledge gap on visual enrichment for captive parrots and their well-being effects on other bird species (e.g. Coulon et al., 2014), two naturalistic and non-naturalistic visual stimulus were chosen. The naturalistic visual stimulus was a collection of videos showing unrelated kea in several contexts (zoos and wild environment) and the non-naturalistic counterpart was an animated film (following the premise that novel, and fast-changing visual stimuli may be relevant characteristics (Wells, 2009; e.g. Jones et al., 1996).

To determine the enrichment potential of these stimuli, the behaviour of captive kea was measured and compared while exposed to these cues. Improving upon past studies that focused on a single behaviour, this study investigated the general behaviour of captive kea. To assess sensory stimulation as enriching there should be an increase of natural, species-appropriate behaviours, an increase of behaviours associated with positive well-being and a decrease of behaviours associated with negative well-being. Furthermore, subjects' attention towards the stimuli was analysed and used as a proxy for the level of intrinsic reinforcement (longer duration of attention to the device would be considered as more reinforcing) and to determine habituation to the stimuli.

## 3.2 Methods

Experimental protocols and data collection took place at Paradise Park, Hayle, UK (50.178°N, 5.425°E) between February and April 2016. Paradise Park is member of EAZA and houses the UK office of the World Parrot Trust. The Park is open to the public 364 days a year from 1000 until 1800 during summer months and 1600 during the winter months.

### 3.2.1 Subjects

Nine kea housed in five enclosures took part in this study (Table 3.1). Eight kea were kept as breeding pairs and the ninth, called Newton, was housed individually. During summer (April – September), Newton is kept in an indoor enclosure 1.65m wide, 1.8m long with a slanted roof (height 2.6 – 2.35m; Figure 3.1A) in a room where a macaw (*Ara ararauna*) and a cockatoo (*Cacatua moluccensis*) were also kept year-round; smaller parrots also shared the room part-time during the day. During winter, Newton is moved to an indoor enclosure 1.2m wide, 2.9m long, and 1.8m tall (Figure 3.1B) in a building housing other parrots. Newton was the only kea visible to the public his participation in a show. Both of Newton's enclosures had perches, easibed© (Easibedding, 2018) substrate, and metallic bowls for food and water. Newton was fed as the other kea during winter, but his diet was

modified during spring and summer: he received a handful of fruit in the morning, followed by almonds and seeds during his routine, and a final weighed feeding of Kaytee© and fruit after the show. Keepers sometimes provided metal cages or cardboard boxes filled with cardboard or newspaper as putative enrichment for Newton.

The other kea were housed as male-female pairs in two separate areas of the park. Two pairs were housed in two outdoor enclosures 1.9m wide, 5m long and 2m tall (enclosures 221 and 223, Figure 3.1 E-F). These enclosures were part of an outdoor, off-show set of six cages. The enclosures not housing kea contained breeding pairs of cockatoos and macaws. Kea pairs were in visual and auditory contact with each other and with the other species. The two other kea pairs were housed in two outdoor enclosures 1.75m wide, 5m long and 2.1m tall (enclosures 81 and 83, Figure 3.1 C-D) as part of a six-enclosure arrangement. The enclosures not housing kea contained macaws, cockatoos, lorikeets, and Amazon parrots. The two kea pairs were in visual and auditory contact with each other and with the other species. These four enclosures had sand as substrate, wooden branches for perching, and metallic food and water bowls. Enclosures 81 and 83 had one wooden nest box each. Enclosures 221 and 223 had one wooden nest box each with an additional nesting compartment made of concrete. Kea pairs were fed a mixture of Kaytee©, fresh fruit once in the morning. The only putative enrichment these eight kea received was fresh browse, branches, or produce (classified as enrichment by the zookeepers as they promoted behaviours such as chewing and were provided outside of their regular feeding schedule). Kea had been exposed to puzzle feeders to test their problem-solving abilities for historic TV filming but had not been formally tested in scientific studies. Specifics of these devices were not available beyond zookeepers' descriptions of "puzzles, boxes and toys".

Table 3.1 – List of kea at Paradise Park. All birds took part in this experiment. All kea were captive born and hand-reared[13] apart from P631, whose rearing history was not available.

| Kea | Enclosure | Age (years) | Sex |
|---|---|---|---|
| Newton | PH / ST2 | 6 | Male |
| P2309 | 81 | 5 | Male |
| P2209 | 81 | 6 | Female |
| P2310 | 83 | 5 | Male |
| P2208 | 83 | 6 | Female |
| P2379 | 221 | 5 | Male |
| P2308 | 221 | 5 | Female |
| P631 | 223 | 30 | Male |
| P1748 | 223 | 29 | Female |

[13] Hand-rearing implicates removing kea chicks from their nests to be fed and taken care of by zookeepers; relevant as wild, hand-reared, and parent-reared parrots have behavioural differences (e.g. Schmid et al., 2006).


Figure 3.1 – Kea enclosures at Paradise Park. A: Newton's enclosure during the summer season. B: Newton's enclosure during the winter season. C: Area where enclosures 81 and 83 were located. D: Inside view of enclosures 81 and 83 (both were identical). E: Area where enclosures 221 and 223 were located. F: Inside view of enclosures 221 and 223 (both were identical).

### 3.2.2 Stimuli and playback devices

Kea were exposed to naturalistic and non-naturalistic visual and auditory stimuli. Naturalistic visual stimuli were videos from YouTube and from the researcher's media library showing kea in the wild or in captive settings. Non-naturalistic visual stimuli were scenes of the animated film Río (20$^{th}$ Century Fox, 2011), chosen as the animation and colour contrasts were novel to kea (both in captivity and historically in the wild) and due to their apparent preference by domestic birds (Clarke and Jones, 2000). Short (<1min) kea vocalisations (as per Schwing et al., 2017) formed the naturalistic auditory stimulus. As the total duration of these clips totalled less than two minutes of audio, they were arranged as a 15-min audio file (clips were spaced out and the gaps between clips were intentionally muted). The non-naturalistic auditory stimuli were the top 50 songs in New Zealand according to Spotify at the time of testing.

While the sensory capacities of kea have not been directly investigated, they can recognise 2D, non-animated images on a display (Wein et al., 2015) and, following from the research of Schwing and colleagues (2017), wild kea behaviourally reacted to conspecific calls. Thus, it is believed that kea should perceive the previous stimuli.

Two playback devices were used: a first-generation iPad© mini (Apple, 7.9-inch diagonal, LED-backlit IPS display, 1024x768 resolution at 163 pixels per inch, 378 cd/m$^2$ brightness) and a convertible Ultrabook (Lenovo Flex 2 14, 14-inch diagonal LED-backlit IPS display, 1920x1080 resolution at 157 pixels per inch, 220 cd/m$^2$ brightness).

### 3.2.3 Experimental protocols

The experiment was divided in two phases: baseline and treatment. This design qualified as a multiple-treatment design as the stimuli were alternated across days (Alligood et al., 2017). Multi-treatment designs are helpful in zoo-based research as they "rule out extraneous events as causes of behaviour change, because these would tend to influence all treatment conditions similarly" (Alligood et al., 2017). The baseline phase was implemented to observe kea's behaviour with the devices switched off. During the treatment phase, playback devices were turned on and delivered one of the four stimuli for fifteen minutes. All conditions were to be delivered for five days (but see Section 3.3.1). The baseline phase was provided first. The days in which treatments were provided were pseudo-randomised, ensuring that the same stimulus was not provided for more than two consecutive days. Because kea pairs in enclosures 81 and 83 and 221 and 223 were in auditory contact, on days of auditory stimuli, both pairs received the same treatment (naturalistic or non-naturalistic) as they could hear the sound from the neighbouring pair's device.

An important experimental decision was treatment duration. Other studies on avian sensory enrichment have provided stimuli for: 20 min (Clarke and Jones, 2000), 25 min (Williams et al., 2017), 30 min (Keeling and Hurnik, 1993) and 60 min (Coulon et al., 2014). Whilst not a study on enrichment or well-being, Schwing et al. (2017) played 5 min of auditory stimuli to wild kea with an additional 5 min of pre- and post-treatment behavioural data collection (without providing a rationale for these durations). As a conservative approach, a modification of Schwing and colleagues' (2017) method was adopted: kea in this study received sensory stimulation for 15 min. Behavioural data obtained from these 15 min are not suggested to be representative of the subjects' daily activity patterns. The scope of this experiment was to evaluate stimuli as enrichment by behaviours displayed during their presentation under the assumption that presenting them at different times or for different durations should result in similar effects (see Alligood et al., 2007).

A session started with the researcher placing a playback device in front of the target enclosure less than one meter away and a recording device further away to maximise field of view (no equipment was ever inside the enclosures). The experimenter then started the recording and playback devices and immediately left the area. An "experiment in progress" sign was placed to ensure no staff entered the area during a session. After 15 minutes, the experimenter returned, turned off and retrieved all devices. Kea were video recorded using a Sony Cybershot digital camera and a Sony Handycam once per day. Experimental protocols were performed at least an hour after the morning feed but not on days with adverse weather conditions.

### 3.2.4 Behaviour coding and analysis

Video recordings started as soon as the playback devices were turned on. However, when analysing videos, it was noted that kea were attentive to the researcher upon him getting close to the enclosure, setting up the devices, leaving the area and upon his return. To minimise confounding effects from the researcher's presence (social enrichment), behaviour data were coded from 10 out of the 15 min (using the sound of the main doors being locked / unlocked as indicator of the researcher's presence / absence).

A species-specific ethogram (Table 3.2) was adapted from an existing kea ethogram developed by the Messerli Research Institute, Austria. Two behaviours, pacing and chewing wires, were added based on the researcher's anecdotal observations of the study subjects and the literature on psittacine abnormal behaviour (Chapter 1.6.1.4). All behaviours were classified as states and were coded following a continuous sampling protocol using the Observer© XT 10 (Noldus) for each individual.

Statistical analyses were selected based on the methods of Williams et al. (2017) given the similarity between objectives and protocols to those in the present study. However, as behaviours were classified as states, behaviour durations instead of frequencies were obtained. Data were tested for normality using Shapiro-Wilk tests. Normally distributed data were analysed using a repeated-measures one-way ANOVA. Non-normal data were analysed using Friedman's ANOVA. Post-hoc t-tests were used to identify stimuli differing from baseline data using a significance level of $p<0.01$ after Bonferroni correction. Duration of "Attentive to playback device" is presented separately to explore subjects' interest in the stimuli across time as a way of assessing habituation and intrinsic motivation. These data were analysed in chronological order (i.e. a mean for the first presentation of one stimulus, a mean for the second presentation, and so on for all stimuli). A repeated measures, one-way ANOVA was performed with the five chronological data groups for each stimulus to determine effects of presentation day on attention to the device. All statistical tests were performed on SPSS 24 (IBM, 2017).

Table 3.2 – Kea ethogram. State behaviours based on a species-specific ethogram developed by the Messerli Research Institute, Austria.

| Behaviour | Description |
|---|---|
| Affiliation | Preening conspecific, kea standing still with body contact, feeding conspecific, mating behaviours including wing display or whistling. |
| Aggression | Kea displacing conspecific (moving to the exact location occupied by another kea who moves away), pursuing conspecific beyond the previous location of the chased bird, fighting (distinguished from play due to its high-energy and distress calls). |
| Attentive to playback device | Kea standing still on the ground one body-length away from the enclosure wall closest to the playback device or hanging from the mesh of the wall closest to the device. |
| Bathing | A kea standing in or on a water bowl submerging body parts or splashing water on self. Often recognised by head submersion and flicking upon resurfacing. |
| Chewing wire | Biting the wire from enclosure walls or roof. |
| Climbing | Using beak and feet to navigate the mesh walls or roof. |
| Drinking | Drinking water from the water bowl. |
| Eating | Foraging for food spilled on the floor or from the food bowls. Eating food from bowl or foraging on the floor for spilled items. |
| Locomotion | Flying, walking on perch or ground, or running on ground (not chasing a conspecific) in the enclosure. |
| Object manipulation | Interacting with a non-edible object from the enclosure by using beak or feet. Often includes tossing, holding, or chewing. |
| Out of sight | Kea out of the viewing area of the recording device. |
| Pacing | Stereotypical behaviour where a kea would walk or run back and forth, following the same route and usually with the head tilted at an angle at each endpoint. |
| Preening | Maintenance of self's plumage with beak. |
| Play behaviours | Kea engaging in "play fighting", using kicks, pinging one another, rolling onto the back, and hopping on the ground. May be accompanied by warble or screech vocalizations. Non-aggressive as kea put themselves into vulnerable positions, and do not try to flee. |
| Resting | Standing inactive, sleeping. |

## 3.3 Results

### 3.3.1 Video data

Table 3.3 shows the number of sessions available for each enclosure and treatment. During the baseline phase, 250 minutes of video data were collected for all enclosures and birds. Non-naturalistic sounds totalled 230 minutes of video data for all enclosures and birds but data for enclosures 221 and 223's fifth day were not available. Non-naturalistic videos totalled 200 minutes of video data for all enclosures and birds. There were no data for Newton's fifth day or enclosures 221's and 223's fourth and fifth days. Naturalistic sounds totalled 240 minutes of data. Data were not available for day 5 of enclosure 83. Naturalistic videos totalled 250 minutes of data. Differences in collected were due to: rain (the equipment was exposed to outdoor conditions during testing), battery failure, movement of the camera (e.g. blown down by wind) or sun's position (resulting in videos with high brightness not allowing to determine its contents).

Table 3.3 –Number of experimental sessions for each enclosure.

| Enclosure / Treatment | Baseline | Naturalistic sounds | Naturalistic videos | Non-naturalistic sounds | Non-naturalistic videos |
|---|---|---|---|---|---|
| 81 | 5 | 5 | 5 | 4 | 3 |
| 83 | 5 | 5 | 5 | 4 | 3 |
| Newton's | 5 | 5 | 5 | 5 | 4 |
| 221 | 5 | 4 | 5 | 5 | 5 |
| 223 | 5 | 5 | 5 | 5 | 5 |

### 3.3.2 Behaviour analysis

Locomotion was the only behaviour that showed a normal distribution according to a significant ($p>0.5$) Shapiro-Wilk test (Appendix 2 includes Shapiro-Wilk test results for each behaviour). Chewing wire, drinking, object manipulation and preening were significantly affected by experimental protocols according to Friedman's ANOVA tests (Table 3.4).

Table 3.4 – Means and ANOVA results for behaviour durations. [+]Locomotion was found to be normally distributed and was analysed using a repeated-measures one-way ANOVA. All other behaviours were analysed using related samples Friedman's two-way ANOVA. Significant outcomes in bold according to $p<0.05$.

| | Mean duration (s) | | | | | Test statistic $\chi^2(4)$ | p |
|---|---|---|---|---|---|---|---|
| | **Baseline** | **Naturalistic sounds** | **Naturalistic videos** | **Non-naturalistic sounds** | **Non-naturalistic videos** | | |
| Affiliation | 0.0 | 0.0 | 0.0 | 0.0 | 8.30 | 8.000 | 0.092 |
| Aggression | 0.08 | 0.08 | 0.35 | 0.02 | 0.07 | 6.380 | 0.173 |
| Attentive to playback device | 51.13 | 97.83 | 93.07 | 66.32 | 110.22 | 7.111 | 0.130 |
| Bathing | 1.91 | 0.0 | 0.0 | 0.0 | 0.0 | 4.000 | 0.406 |
| **Chewing wire** | **0.87** | **0** | **1.03** | **0.11** | **0.41** | **14.080** | **0.007** |
| Climbing | 9.18 | 7.41 | 7.90 | 7.93 | 5.16 | 6.764 | 0.149 |
| **Drinking** | **0.06** | **0.0** | **0.28** | **0.0** | **0.0** | **10.857** | **0.028** |
| Eating | 0.0 | 5.10 | 3.72 | 0.26 | 3.15 | 6.919 | 0.140 |
| Locomotion[+] | 20.59 | 19.04 | 18.68 | 15.35 | 18.42 | $F_{4, 32}=0.306$ | 0.872 |
| **Object manipulation** | **0.67** | **0.50** | **5.99** | **2.84** | **2.61** | **9.658** | **0.047** |
| Out of sight | 311.81 | 274.99 | 288.15 | 298.58 | 319.87 | 2.222 | 0.695 |
| Pacing | 15.28 | 5.14 | 6.01 | 15.09 | 11.55 | 5.167 | 0.271 |
| Playing | 0.0 | 0.04 | 0.04 | 0.0 | 0.03 | 4.000 | 0.406 |
| **Preening** | **5.34** | **10.07** | **11.62** | **1.39** | **5.42** | **12.107** | **0.017** |
| Resting | 51.46 | 136.41 | 78.80 | 157.09 | 72.29 | 9.156 | 0.057 |

Wilcoxon's pairwise comparisons were performed (with a Bonferroni correction for multiple comparisons) on behaviours that showed significant Friedman's ANOVA results (chewing wire, drinking, object manipulation and preening). Behaviour durations were not significantly different between treatments ($p>0.05$, adjusted significance) for any behaviour except for preening duration, which was significantly different between non-naturalistic sounds and naturalistic videos ($p=0.037$, adjusted significance; see Appendix 2 for full pairwise comparisons' statistics).

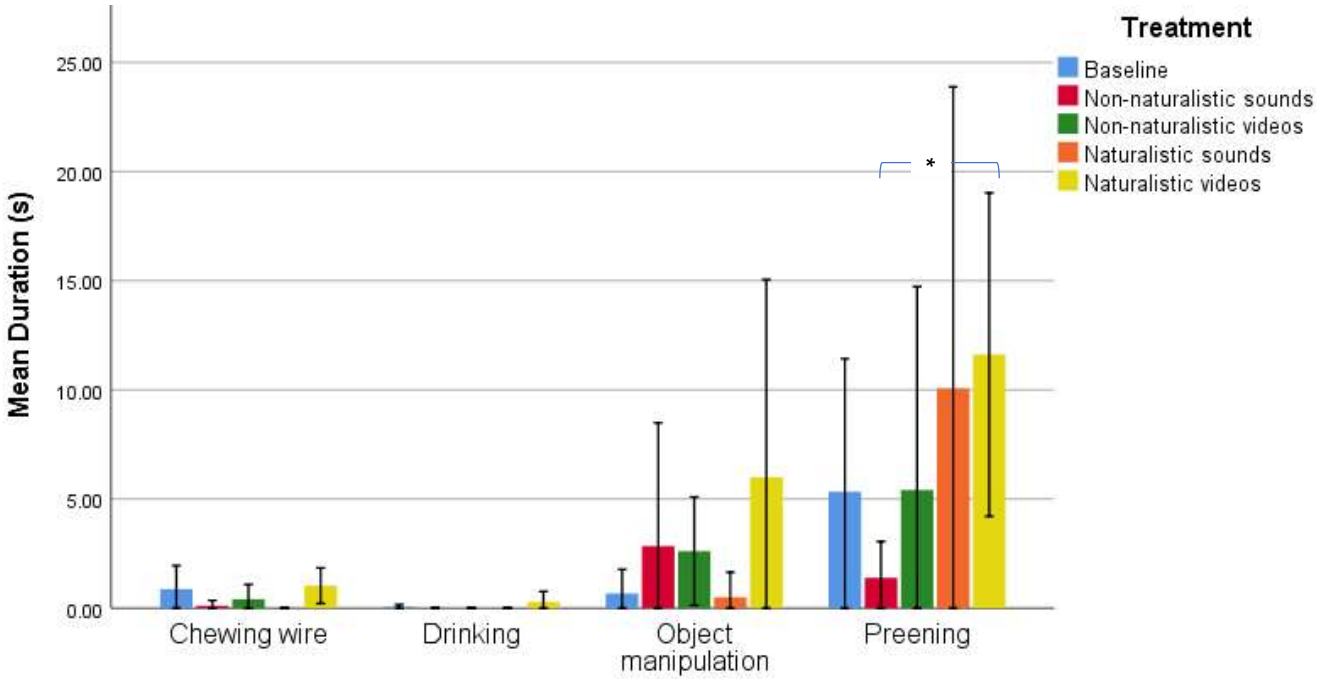



Figure 3.2 – Mean durations and standard errors of kea (N=9) behaviours found to be significantly different across treatments. Error bars: 95% confidence interval. Post-hoc tests showed that there was only a significant difference between naturalistic videos and non-naturalistic sounds on preening behaviour.

### 3.3.3 Attention to playback devices

Attention to playback devices was not significantly different across treatments (Table 3.4). Descriptive data (Figure 3.3) showed that kea spent more time near a playback device when naturalistic videos were being presented. Kea spent the least amount of time near the playback device during the baseline phase.

After chronologically reorganising "attention to device" duration data per day (see Section 3.2.4) repeated measures, one-way ANOVAs, found no significant effects during baseline ($\chi^2(4) = 3.535$, $p=0.473$) and non-naturalistic videos ($\chi^2(4) = 1.600$, $p=0.809$). Attention to device during naturalistic sounds ($\chi^2(4) = 12.538$, $p=0.014$) and videos ($\chi^2(4) = 15.618$, $p=0.004$) and non-naturalistic sounds ($\chi^2(4) = 9.600$, $p=0.048$) significantly differed across time. Figure 3.4 shows the fluctuation of attentive to device durations across the five experimental days for each type of stimulus.

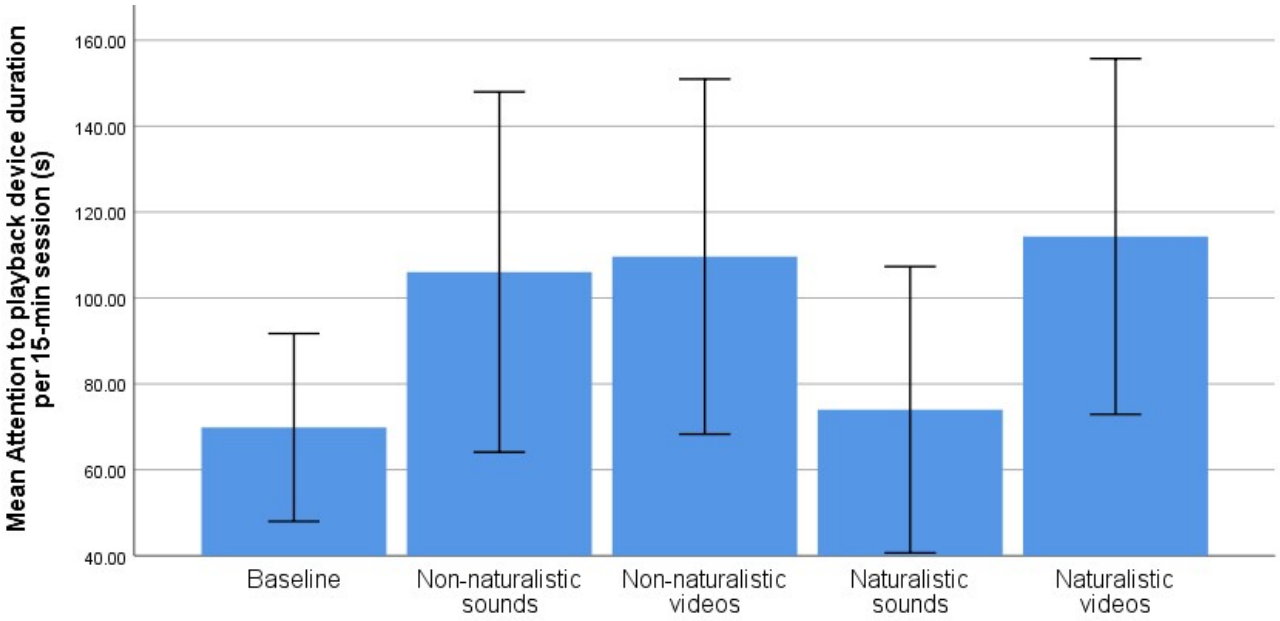



Figure 3.3 – Mean durations of attention to playback devices across treatments and birds (N=9). Error bars: 95% confidence interval.

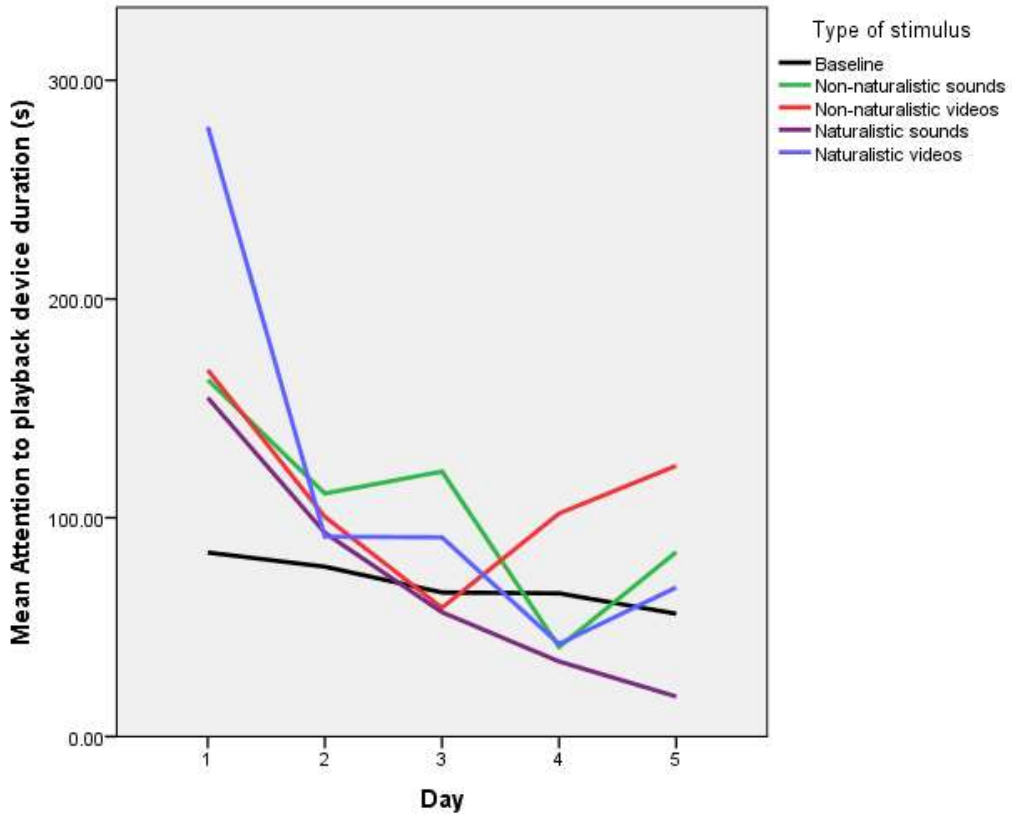



Figure 3.4 – Mean attention to playback devices across experimental days. Data for baseline and naturalistic videos showed no significant differences across days.

## 3.4 Discussion

The responses of captive kea to different sensory stimuli were recorded to test the hypothesis that their behaviour would be affected, potentially improving their well-being. Behaviour analyses showed that stimuli had a significant effect on subjects' behavioural repertoire via differences in drinking, chewing wire, preening and object manipulation durations. The well-being impact of these behavioural changes is discussed next.

### 3.4.1 General behaviour

Drinking was not observed in three of the five treatments and had a low duration in the other two. Only naturalistic videos were associated with an increase in drinking behaviour. Drinking has been shown to (non-significantly) increase when parrots are exposed to putative foraging enrichment due to an increase in species-specific behaviours, resulting in a time-budget similar to that of wild conspecifics (Coulton et al., 1997). However, excessive drinking behaviour could become polydipsia and potentially compromise well-being, as polydipsia has been discussed as an adjunctive behaviour when food rewards are provided at specific schedules (Falk, 1971). Given that there was no food being delivered in this experiment, polydipsia appears unlikely.

Preening behaviour shifted from baseline levels in two directions: it increased when kea received naturalistic stimuli and decreased or remained constant when non-naturalistic stimuli were being delivered. Preening is a natural, energy-consuming behaviour in which birds spend much of their time (Moreno-Rueda, 2017; Walther and Clayton, 2005) with benefits like plumage maintenance and waterproofing (Moreno-Rueda, 2017). Williams and colleagues (2017) tested ten parrots of different species by exposing them to classical music, rainforest sounds, parrot vocalisations and radio talk. Preening and calm vocalisations were the only behaviours that showed significant differences: parrots preened the least when no stimuli were provided and the most during rainforest and talking radio sounds. Amorim and Schetini (2011) provided foraging and physical enrichment to Amazons (*Amazona aestiva*), also finding significant differences in preening behaviour. Amazons preened non-significantly more during the enrichment phase than before receiving enrichment and significantly more after enrichment provision. The changes in preening behaviour in these two studies could be discussed as a positive effect, indicating that this study's subjects expressed a natural, normal behaviour. It is also possible that an increase in preening behaviour results in over-preening, but neither Amorim and Schetini (2011) nor Williams and colleagues (2017) reported this. Captive parrots are susceptible to developing abnormal behaviours, some because of the excessive performance of a normal behaviour (Van Zeeland et al., 2009). Feather damaging behaviour develops from the over-expression

of preening behaviour, has been linked with medical problems, and is indicative of poor well-being (Van Zeeland et al., 2009). De Almeida and colleagues (2018) reported a decrease in preening behaviour in macaws (*Ara ararauna*) because of their enrichment regime, which they described as a positive effect on well-being. One of their subjects already suffered from feather-picking whereas none of the kea in this study exhibited feather damaging behaviour or were reported to have medical problems. Also, kea had not been reported to engage in feather damaging behaviour before or after this experiment.

Chewing (enclosure) wires was also significantly affected by sensory stimulation. Durations in all conditions except naturalistic videos were lower than baseline levels. Chewing wire is considered an oral stereotypical behaviour, predicted to be a result of frustrated foraging behaviour (Meehan et al., 2004) and thus associated with poor well-being. Protocols from other parrot studies have been described as enriching due to a reduction in oral stereotypies (e.g. Meehan et al., 2004; Polverino et al., 2012). Sensory stimulation elicited a positive effect on kea well-being by reducing chewing wire behaviour across all treatments except naturalistic videos. It is possible that kea perceived naturalistic videos (i.e. 2D representations of kea) as a frustrating social manipulation and thus still performed chewing wire behaviour. While it is not possible to establish how kea perceived the stimulus, research has shown that social stimulation (i.e. social housing) decreases the frequency of oral stereotypies in parrots (Polverino et al., 2012), thus hinting that other, currently unknown, reasons may exist to explain why naturalistic videos had a different effect.

Durations of object manipulation were longer in all treatments compared to naturalistic sounds (Figure 3.2). In the wild, kea are highly extractive foragers, often scratching, drawing, scraping, pushing, and opening objects (Huber and Gajdon, 2006). Meehan and Mench (2002) demonstrated how foraging and physical enrichment increased interaction with novel objects, with authors discussing this result in terms of a decrease in fearfulness and thus a well-being improvement. It is also possible that an increase in exploration could be indicative of poor well-being. For example, Lewis (1999) induced frustration in pigs by fasting them and then exposing them to two types of (empty) feeders: open-feeders (i.e. hunger and no food available) and feeders with a lid (hunger and problem solving). Behavioural analyses showed that pigs' activity levels and feeder manipulation responses increased (i.e. higher exploration). Authors recognised that frustration and hunger are two variables that confound each other: it was not possible to determine which of the two caused the behavioural responses. Kea in the present study were not deprived of their regular resources (e.g. food, water) thus suggesting that the increase in object manipulation does not represent a negative well-being effect. Following the premise that frustration from a

stressor can cause redirected behaviour (e.g. Waters et al., 2002), kea would be predicted to be motivated to perform object manipulation towards the playback device or certain aspect of the stimuli. For example, naturalistic videos and sounds showed conspecifics or their vocalisations, thus kea might be motivated to physically interact with the kea depicted by these stimuli but would have to redirect these behaviours. However, the fact that object manipulation also increased with non-naturalistic stimuli seems to indicate that object manipulation is not a redirected behaviour, as kea would have to be able to identify the film and songs as relating to something that they can manipulate. This possibility cannot be completely ruled out with the methods and data from this study, unfortunately. A follow-up study comparing non-accessible devices with an accessible variant could be performed to identify if behaviour is indeed redirected or not.

### 3.4.2 Intrinsic reinforcement and habituation to stimuli

Subjects' interest in auditory and visual stimuli was measured by quantifying the time spent near the devices. From casual observations prior to the experiment, it was known that kea spent most of their time either in their nest box or perching on branches. By standing close to the playback devices, subjects were hypothesised to be interested in the stimuli. Attention to playback devices had its lowest level during the baseline phase and increased in all four treatments, with naturalistic videos showing the maximum value, suggesting that subjects were interested in this treatment. However, attention to playback devices did not differ between stimuli, even when compared to the baseline phase. Robbins and Margulis (2016) provided auditory stimuli to turacos (*Musophaga rossae*), mouse birds (*Colius stratus*) and starlings (*Lamprotornis superbus*), finding that subjects rarely investigated auditory sources in both playback and muted conditions but failed to discuss this result. Kea's responses were probably due to their curiosity and overt exploration (Diamond and Bond, 1999; Huber and Gajdon, 2006).

Habituation, defined as the decrease in responses resulting from repeated stimulation (Harris, 1943) has been identified as a factor of enrichment effectiveness (Tarou and Bashaw, 2007). Attention to devices was analysed across time to determine habituation effects. Attention duration to naturalistic videos and non-naturalistic sounds showed significant differences across time: interest in these stimuli was highest on day 1 and decreased throughout the experiment. Interest in naturalistic sounds went below baseline levels at the end of the study. This indicates that kea were most interested in the stimuli at the beginning of the experiment and lost interest gradually. Tarou and Bashaw (2007) explained this habituation pattern based on how intrinsic reinforcement often habituates across consecutive presentations. Research has shown that intermittent, rather than

continuous, presentations minimised habituation (Anderson et al., 2010). Besides the change in frequency, another way to prevent habituation is using novel stimuli instead of repeating the same audio / video (Tarou and Bashaw, 2007).

### 3.4.3 Final remarks

Environmental enrichment has the objective of improving the well-being of captive animals. Sensory enrichment opportunities are less prominent in the literature but have been shown to positively affect animal behaviour (Robbins and Margulis, 2016; Williams et al., 2017). This study showed that the behaviour of captive kea appeared sensitive to the provision of sounds and videos. Some of the behavioural changes may be reflective of an improvement in well-being as chewing wire, a behaviour associated with poor well-being in parrots (see Chapter 1.5.1), decreased. Locomotor stereotypy in the form of pacing was also assessed in the study but it was not significantly modified by the protocols. Looking at the descriptive statistics for this behaviour (Table 3.2), there was a reduction in the duration of pacing when compared to baseline levels, a promising result warranting further research. Furthermore, natural, normal behaviours (drinking and preening) were also promoted by sensory stimulation.

Conclusions are limited to the specific stimuli provided in this study and further research into the specific characteristics of videos and sounds that influence captive kea behaviour is recommended. Naturalistic audio clips (i.e. kea vocalisations) were shared to the researcher by an external scientist. These audio files had short durations, so they had to be merged to create a single file of equal duration to the other stimuli. As a result, there were gaps with no sounds being emitted between each kea vocalisation (these were intended and not indicative of defective stimuli). It is possible that these silent gaps affected kea behaviour. Research on other species has shown that subjects significantly avoided an auditory stimulus containing silent fragments and became more active with a continuous (no silent fragments) delivery (Talling et al., 1998). This finding may suggest that kea could show avoidance responses towards naturalistic sounds. Looking at the data on Attention to the Playback Device (Figure 3.3), kea were less interested in naturalistic sounds than any other stimuli, but they still showed more interest in being near the playback device when compared to baseline conditions).

This study showed that auditory and visual stimuli have potential as enrichment opportunities for kea, given the observed behavioural changes. The fact that kea seemed to habituate to five days of each stimulus over a month indicates the need to plan and design an enrichment protocol varied on both, frequency and type of stimulus. Further

recommendations for future work on sensory enrichment are studies utilising a larger sample size and, if possible, studying kea in social groups to determine if there is a social component associated to the behavioural responses to sounds and videos (e.g. social play as per Schwing et al., 2017a).

### 3.5 Conclusions

- Preening, drinking, chewing wire and object manipulation behaviours were affected by exposure to visual and auditory stimuli.

- There was a non-significant decrease in pacing behaviour, suggesting that sensory stimuli may have a positive impact on captive kea well-being; further research is warranted to investigate this possibility.

- Kea were assumed to be interested in the playback devices by standing near them. Interest non-significantly increased from baseline levels.

- Naturalistic and non-naturalistic videos had the highest interest on day one. However, kea became habituated to the stimuli during the experiment as interest decreased across sessions.

# Chapter 4. Evidence of contrafreeloading in a group of captive kea

## Abstract

When animals are kept in captivity, foraging behaviour can be constrained by the way in which food is delivered. Usually, this delivery is based on providing free food (e.g. food in trays or bowls). The optimal foraging theory would support this method of feeding, as animals are thought to maximise rewards and minimise efforts. However, there is evidence that some animals will, given the choice, work to obtain a resource even if it is simultaneously freely available: a phenomenon called contrafreeloading. Contrafreeloading is believed to happen as it allows animals to obtain resource information that could be useful in the future or the work performed to access resources could be intrinsically reinforcing. In the context of captivity, denying working opportunities to animals shown to contrafreeload might elicit frustration and negatively impact their well-being. Food delivery for a group of captive kea was modified to determine if contrafreeloading was performed and to assess the intervention as foraging enrichment. First, baseline foraging behaviour was analysed to determine tray preferences and foraging durations. Food presentation was then modified by adding rocks or wooden blocks to increase foraging time (i.e. work for food). Foraging durations in trays with and without objects were found to be statistically equal (Wilcoxon's signed-rank test: $Z=-0.405$, $p=0.686$), suggesting that kea contrafreeloaded. Behaviour comparisons did not allow to evaluate the intervention as enrichment as there were no significant differences between treatments. However, (non-significantly) higher foraging durations and observations of play and object manipulation behaviours in the foraging intervention showed the potential of this intervention to promote behaviours associated with positive well-being.

## 4.1 Introduction

Chapter 1 provided an account of how explorative, curious, and playful kea have been reported to be. These behavioural traits and their wild environment have influenced kea's foraging behaviour to be "not only opportunistic and innovative but also highly extractive or, when humans artefacts are involved, massively destructive" (Huber and Gajdon, 2006). Foraging behaviour dominates wild parrots' activity budgets (Birchall, 1990) and it appears to be restricted in captivity. Food for captive parrots is often provided in a single dish (Coulton et al., 1997), limiting natural foraging behaviours performed to search and locate food (Keiper, 1969). For example, modifying food presentation from one (food in bowl) to three (food in bowl plus two foraging devices) opportunities had a positive effect on captive parrot well-being, assessed by an increase in species-specific behaviours (Coulton et al., 1997).

Manipulation of feeding methods is described as a possible way to enrich captive animals (Newberry, 1995). Foraging enrichment devices designed to increase foraging and locomotion behaviours have been shown to reduce the development and intensity of abnormal repetitive behaviours in parrots (Meehan et al., 2004; Amorim and Schetini, 2011). Avoiding simplistic feeding methods such as "food in a bowl" might also be relevant to fulfil some species' apparent need to work for food or contrafreeload. Chapter 1.2.6 discussed the contrafreeloading phenomenon as a framework for the apparent need of captive animals to perform behaviours associated with working for a reward and listed the species that have been shown to contrafreeload in captivity (Table 1.1), with contradicting evidence towards the contrafreeloading behaviour in captive parrots.

Rozek and Millam (2011) provided Amazons (*Amazona amazonica*) pellets in two feeders, one without a lid (free food) and one with a lid. Authors concluded that Amazons did not contrafreeload as they only retrieved pellets from the feeder with no lid. However, they reported that 17.06 g (feeder with no lid) and 0.57 g (feeder with lid) of pellets were removed from each feeder: the fact that removed pellets from the feeder with a lid was not zero indicates that amazons did contrafreeload, as they accessed non-free food in the presence of free food. Authors seemed to agree, as they also mentioned that "prior experiment effects may have reduced contrafreeloading", "reduced" indicating that contrafreeloading indeed occurred. Coulton and colleagues (1997) provided putative foraging enrichment to macaws (*Ara rubrogenys, A. chloroptera*), thick-billed parrots (*Rhynchopsitta pachyrhyncha*), and lorys (*Lotius garrulus*) in the form of two wooden devices storing 50 concealed food rewards in either constant (one reward per hole) or variable (five rewards in ten holes) configurations. Parrots were considered to contrafreeload based on their interaction with these devices while their daily diet was simultaneously available in a food bowl. Authors failed to discuss

the confounding effect of different food items as the regular diet included “fruit, vegetables, nuts, seeds, bread and eggs” but the feeders only included seeds or beans, thus invalidating authors’ claim that “identical free food was available in their food bowls”. The study also failed to acknowledge inter-specific differences that could affect their results (e.g. *Lotius spp.* being distinctively nectarivorous, Cabana and Lee, 2018). Van Zeeland et al. (2010) tested if individually housed grey parrots (*Psittacus erithacus*) with and without feather damaging behaviour contrafreeloaded when given food bowls (free food) and non-described foraging toys. Parrots were found to contrafreeload, as they obtained food from the foraging toys whilst the food-containing bowls were also present. Parrots displaying feather damaging behaviour were found to consume more food from the foraging toys than parrots with no feather damaging behaviour, suggesting that feather-damaging parrots had a higher drive to perform foraging behaviours, thus highlighting the putative well-being relevance of providing opportunities to display foraging behaviours.

Generally, when animals forage in the wild, they perform some level of work such as searching, extracting, or hunting. Kea, being extractive foragers, may be acquainted with working for food. Anecdotal evidence showed that kea obtain food by opening rubbish bins with obstructed lids (Diamond and Bond, 1999). While kea’s extractive foraging behaviour is probably adaptive to their wild environment, it is not known whether kea would actively prefer to access food by extraction / problem-solving or to avoid these challenges and obtain (free) food directly. Kea’s behaviour is overtly explorative, given their high levels of neophilia and curiosity (Diamond and Bond, 1999; Huber & Gajdon, 2006). Explorative behaviour has been described as an effective resource to gather information in an uncertain environment (Inglis et al., 1997). This raises the question of whether kea naturally exhibit contrafreeloading as part of their foraging repertoire. Knowing if kea contrafreeload would be relevant for their captive husbandry, as it would open the possibility of incorporating contrafreeloading opportunities to daily feeding routines as enrichment.

Given the limited (and contradicting) evidence on parrot contrafreeloading behaviour, the contrasting behaviour of kea when compared to other parrots, and the possibility of improving captive kea well-being, an experiment was designed to determine if kea accessed non-free food in the presence of free food. The feeding protocol of a group of captive kea was modified by adding objects to one of two feeding bowls with the intention of increasing handling time. Based on kea’s drive to explore, they were expected to contrafreeload by foraging from the tray with added objects. Also, object-related behaviours and increased foraging durations (e.g. van Zeeland et al., 2013) were expected, and these would indicate a positive well-being effect.

## 4.2 Methods

This experiment was conducted in Bristol Zoo Gardens, UK between February and April 2016. Bristol Zoo Gardens is part of the Bristol, Clifton and West of England Zoological Society Ltd. (Charity reg. no. 1104986) and is a member of the British and Irish Association of Zoos and Aquariums (BIAZA), the European Association of Zoos and Aquaria (EAZA), the World Association of Zoos and Aquariums (WAZA), and the World Conservation Union (IUCN).

### 4.2.1 Subjects

At the time of the experiment, there were seven kea at Bristol Zoo (Table 4.1). A male-female pair and their three offspring plus a second male-female pair were housed together, but the second pair was relocated due to aggression (this pair was did not participate in the study). Kea were housed in an outdoor exhibit (Figure 4.1) with wood chips and soil as substrate and a few established shrubs and bushes. A pond and a waterfall provided drinking water, branches were provided as perching sites, and several nest boxes were available for nesting and hiding. Kea were on public display during the zoo's opening hours (0900 – 1700, daily). Food was offered twice per day, in a morning and an afternoon feed. The morning feed included fruits or vegetables mixed with T16 Nutriseed® pellets and seeds on alternating days. The afternoon feed included two of the following options: cheese, peanut butter, yoghurt, boiled eggs, and bread. These items were delivered inside bags or boxes or spread around the enclosure as putative enrichment.

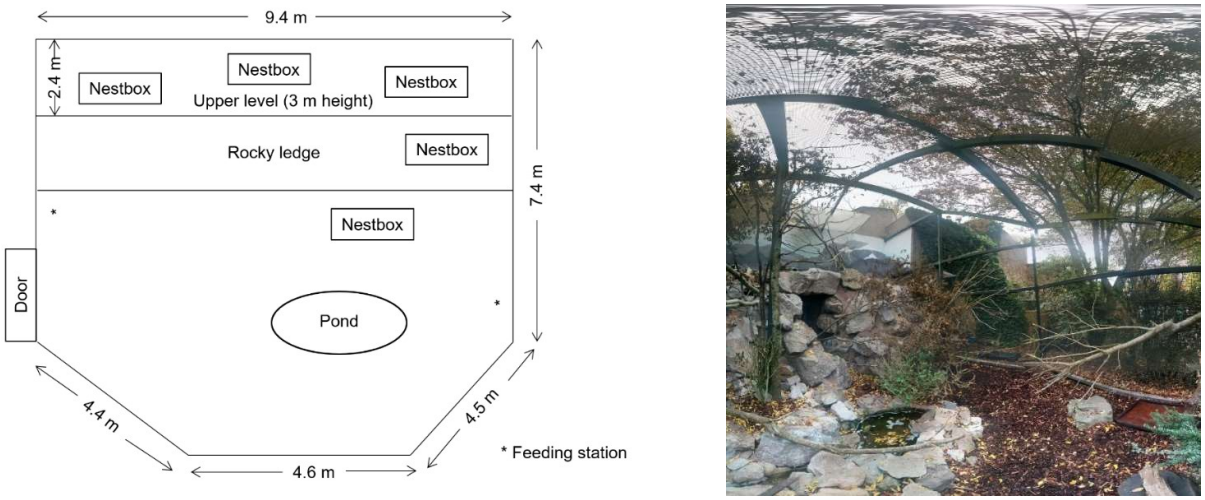



Figure 4.1 – Kea enclosure. Left: schematics and measurements of the enclosure. Right: panoramic, inside view of the enclosure.

Table 4.1 – List of kea at Bristol Zoo. Birds marked with * were housed in the enclosure temporarily but were not included in this study. All kea were captive-bred and parent-reared[14].

| Kea (ring colour) | Sex | Age |
|---|---|---|
| Blue | Male | 8 years |
| Yellow | Female | 8 years |
| Orange | Male | 7 months |
| Red | Male | 7 months |
| Black | Male | 7 months |
| Green* | Male | 27 years |
| Purple* | Female | 12 years |

### 4.2.2 Experimental protocols

The experiment centred around the morning feed, as it showed more consistency across time when compared to the afternoon feed and reduced effects from zoo visitors, as the zoo had fewer guests during this time. Three conditions were provided (Table 4.2). The baseline phase (B) did not involve any interventions. Here, zookeepers divided the morning food into two equal parts in two food trays. Trays were placed on their usual elevated feeding stations in opposite sides of the enclosure and the keeper would leave the enclosure immediately after placing both trays. After one week, trays were placed on the ground instead of the elevated stations as future interventions could result in injured kea if one of the elements to increase the work required to obtain food were to fall down. Phase R involved the addition of rocks into one tray while the tray with no rocks presented food as in Phase B. All other feeding aspects were not modified. Phase W involved the addition wooden blocks into one tray while the tray with no wooden blocks presented food as in Phase B. The tray receiving rocks or wooden blocks was randomised by a coin toss with the condition that no tray received the treatment for three or more consecutive days to prevent location biases. Figure 4.2 shows tray appearance during each phase. Video recordings were used to obtain behavioural data. A Sony Handycam video camera and a Sony Cybershot digital camera were used. Each camera was mounted on a tripod, placed outside of the enclosure and pointed towards each tray. Recordings started when the first food tray was placed in the enclosure and stopped when either all kea stopped foraging for 5 consecutive minutes or if the battery of either camera depleted, whichever happened first. Trays, food items, and occluding objects remained in the enclosure until collected the following morning.

[14] Parent-rearing implicates kea chicks not being removed from their nests to be fed and taken care of by zookeepers; relevant as wild, hand-reared, and parent-reared parrots have behavioural differences (e.g. Schmid et al., 2006).

Table 4.2 – Description of experimental phases with information on phase length and subjects. The difference in phase length was due to kea chewing and spreading wooden blocks around the enclosure to the point keepers had to look for them to be reused. While new cubes could have been introduced, this was predicted to introduce a novelty effect (e.g. Trickett et al., 2009) not present in Phase R.

| Phase | Description | Length | Participating kea |
|---|---|---|---|
| Baseline (B) | Normal feeding. This phase was divided in two: trays placed in their holders and thereafter trays placed on the ground. | 11 days (7 days with trays on the walls in holders, 4 days with trays on the ground) | Blue, Yellow, Orange, Red and Black. (Juveniles absent on Day 4, Orange absent on Day 11, Green and Purple absent). |
| Rocks (R) | Ten rocks (mean weight: 221.75 g) were added to one tray. | 21 days | Blue, Yellow, Orange, Red and Black. (Orange absent for four days., Black absent for eight days, Green and Purple present for twelve days). |
| Wooden blocks (W) | Wooden blocks (mean weight: 50.97 g) were added to one tray. | 14 days | Blue, Red, Orange, and Yellow. (Black was transferred to a different zoo). |


Figure 4.2 - Tray contents in the different phases. a) Tray with morning diet (pellets, fruits, and vegetables) during baseline (B) conditions. b) Tray contents covered by rocks during Phase R. c) Tray contents covered by wooden blocks during Phase W.

### 4.2.3 Behavioural coding

A total of 118 videos were analysed, ranging in duration from 3.6 to 71.9 min. The number of recordings per individual differed since juveniles were temporarily removed from the enclosure for veterinary purposes and one of the juveniles was later sent to a different zoo. Videos were transferred into a computer and analysed with The Observer XT 10 (Noldus©). Videoclips were analysed following a continuous, focal animal sampling protocol for all subjects. Table 4.3 lists and describes coded behaviours. Durations (state behaviours) and frequencies (event behaviours) were transferred to an Excel file.

Table 4.3 – Ethogram used for behaviour coding. Medians were obtained for each behaviour (using individual kea data) except for behaviours marked with * for which means were used due to a high occurrence of null values, resulting in a median of zero.

| Behaviour | Type | Description |
|---|---|---|
| Manipulating tray contents | State | Kea lowering head into food tray and using its beak to move / flick the tray contents. |
| Eating | | Kea consuming food item. |
| Manipulating tray* | | Kea grabbing food tray with beak and attempting / succeeding to displace the tray |
| Manipulating CFL object | | Kea grabbing the added rocks or wooden blocks with beak and chewing them or displacing them, or using feet to grab and manipulate said objects. |
| Removed CFL object* | Event | An added object (rock or wooden block) is removed from the tray by lifting it with beak and flicking / dropping it outside of the tray. |
| Flip tray* | | Kea grasping food tray with beak and flipping it over, spilling the tray's contents over the ground. |

A binary variable called "first chosen tray" (FC) was determined by noting from which tray kea foraged first immediately after being placed in the enclosure during Phase B. Data for FC included far tray (tray on the opposite side of the enclosure's entrance) and close tray (tray closest to the enclosure's entrance). This variable measured if there was a pre-existing preference towards either of the trays that could confound tray preference during subsequent phases. Foraging duration (FD) was calculated by scoring instances in which kea were handling or consuming food from the trays. Behaviour durations were transformed into a proportion of total recording time as the video recordings had variable durations, but absolute behaviour durations are also presented.

### 4.2.4 Data analysis

First, a Fisher's exact test of independence was performed to determine whether the proportions of FC were different among subjects. If Fisher's test was not significant, data for

all kea were pooled and another exact test of goodness-of-fit was run. Exact tests of goodness-of-fit (chosen because FC was a nominal variable and observations and expected proportions were small, McDonald, 2014) were performed with FC data during Phase B to determine if there was a significant preference for either tray. Then, a Wilcoxon signed-rank test was performed to determine if there were differences in the proportions of foraging behaviour at each tray. Repeated G-tests of goodness-of-fit were performed with FC data during Phases R, W (as they are performed in lieu of multiple goodness-of-fit tests; McDonald, 2014) and both phases together to determine if kea preferred to choose first the tray with occluding objects or not. Wilcoxon signed-rank tests were performed with behavioural variables to determine if kea performed each behaviour more (in terms of frequency or duration, see Table 4.3) at either tray. Wilcoxon signed-rank tests were performed to determine if behaviour differed between phases R and W. Finally, a Friedman's test was performed to determine if there were differences in foraging behaviour across phases. Statistical tests were performed at the group level using summary statistics as performing tests at the individual level violates the assumption of independence. Behavioural data used correspond to proportions of video recordings spent performing each behaviour. However, individual data are presented by descriptive statistics throughout the Section 4.3. Significance levels were determined by $p<0.05$ unless otherwise stated. Goodness-of-fit tests and Fisher's tests were performed using McDonald's (2014) spreadsheets. Wilcoxon signed-rank and Friedman tests were performed on SPSS 25 (IBM© 2019).

## 4.3 Results

### 4.3.1 Baseline preferences

The proportions of FC during the Phase B across subjects were not significantly different (Fisher's test of independence, $p=0.304$), which allowed for data to be pooled for group-level analysis. During Phase B, kea did not show a significant preference to choose either tray first (Exact goodness-of-fit test, $p=0.576$). Table 4.4 presents the number of choices per individual and from the group towards each tray.

The Wilcoxon signed-rank test for foraging behaviour duration determined that there was no significant difference between the duration of foraging behaviour at either tray ($z=1.753$, $p=0.080$). Table 4.5 presents the summary statistics of foraging duration at each tray for each subject and for the group.

Table 4.4 – First Choice data during Phase B. N indicates the number of sessions each tray was chosen first. See Table 4.2 for differences in N values.

| Kea | Category | N |
|---|---|---|
| Group | Left tray | 23 |
| | Right tray | 28 |
| Black | Left tray | 5 |
| | Right tray | 5 |
| Blue | Left tray | 7 |
| | Right tray | 4 |
| Orange | Left tray | 5 |
| | Right tray | 4 |
| Red | Left tray | 2 |
| | Right tray | 8 |
| Yellow | Left tray | 4 |
| | Right tray | 7 |

Table 4.5 – Foraging duration data at the individual and group level across baseline sessions.

| Kea | Tray | Relative foraging duration (s) (proportion) | Absolute foraging duration (s) (median) |
|---|---|---|---|
| Group | 1 | 0.29 | 42.07 |
| | 2 | 0.71 | 102.88 |
| Black | 1 | 0.64 | 42.07 |
| | 2 | 0.36 | 23.0 |
| Blue | 1 | 0.21 | 77.36 |
| | 2 | 0.79 | 294.72 |
| Orange | 1 | 0.16 | 20.09 |
| | 2 | 0.84 | 102.88 |
| Red | 1 | 0.25 | 34.17 |
| | 2 | 0.75 | 101.73 |
| Yellow | 1 | 0.34 | 111.04 |
| | 2 | 0.66 | 210.71 |

### 4.3.2 Preferences and behaviours when rocks or wooden blocks were added

During Phase R, kea performed more first choices towards the tray without rocks than the tray with rocks but repeated goodness-of-fit G tests for the group indicated that the difference was not significant (G=0.275, p=0.600). During Phase W, kea chose first the tray with wooden blocks than the tray without them more often, but repeated goodness-of-fit G test for the group indicated that the difference was not significant (G=3.675, p=0.055). Repeated goodness-of-fit G tests for Phases R and W's data pooled together did not show a

significant difference between FC for trays with or without objects (G=0.559, p=0.455). Table 4.6 shows the summary data for FC for each kea and for the group.

Table 4.6 - First Choice data during Phases R, W and both phases. Decimal numbers indicate the proportion of First Choices towards the tray including objects (compared to the tray without objects). Numbers in parenthesis indicate the number of sessions (see Table 4.2 for differences).

| Kea | FC proportion (number of sessions) | | |
|---|---|---|---|
| | Phase R | Phase W | Phases R+W |
| Group | 0.47 (91) | 0.62 (54) | 0.53 (145) |
| Black | 0.46 (13) | NA | 0.46 (13) |
| Blue | 0.42 (21) | 0.71 (14) | 0.54 (35) |
| Orange | 0.70 (17) | 0.69 (13) | 0.70 (30) |
| Red | 0.47 (21) | 0.50 (14) | 0.48 (35) |
| Yellow | 0.31 (19) | 0.61 (13) | 0.43 (32) |

Wilcoxon signed rank tests showed that there were no significant differences in the amount of time spent: manipulating either trays' contents (Z=0.674, p=0.500), foraging (Z=-0.405, p=0.686; Figure 4.3), manipulating the trays (Z=0.365, p=0.715) and flipping the tray (Z=1.604, p=0.109) during Phase R. Wilcoxon signed rank tests showed that there were no significant differences in the amount of time spent: manipulating either trays' contents (Z=0.730, p=0.465), foraging (Z=1.095, p=0.273; Figure 4.3), manipulating the trays (Z=0.730, p=0.465) and flipping the tray (Z=-0.308, p=0.705) during Phase W.

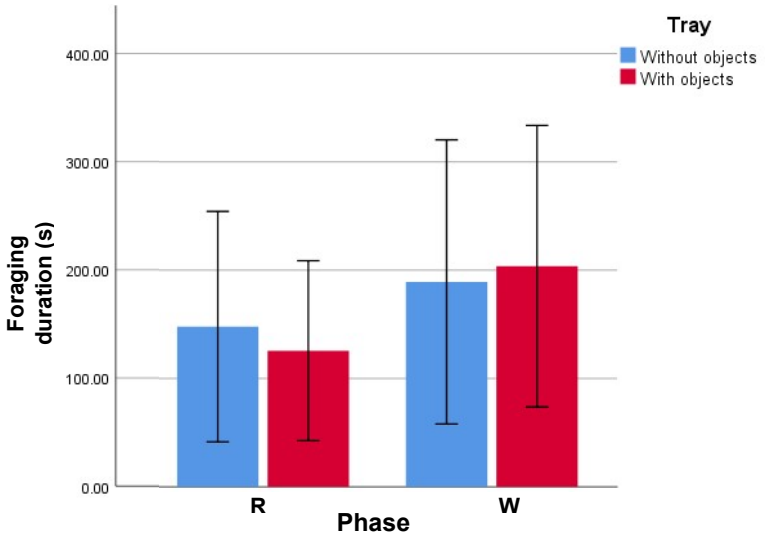



Figure 4.3 – Foraging behaviour duration. Error bars: 95% confidence interval.

Overall, kea interacted more with wooden blocks than with rocks (Figure 4.4). However, a related-samples Wilcoxon signed rank test showed this difference was not significant (Z=1.826, p=0.068). Finally, kea were found to forage for longer durations during Phases R and W than during Phase B (Figure 4.5), but this difference was not significant (Friedman's test, $\chi^2$=4.500, 0.105).

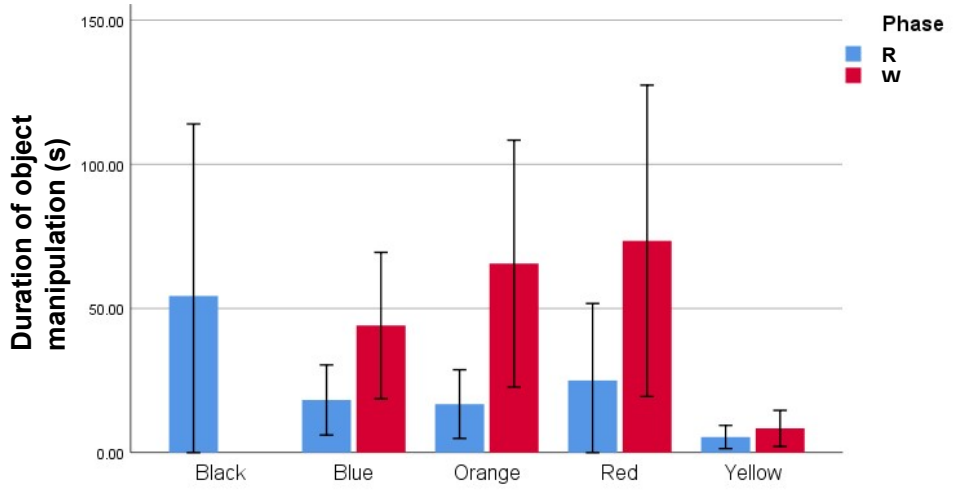



Figure 4.4 – Duration of object manipulation. Bars show mean duration each kea spent interacting with the occluding objects in phases R and W. Black did not participate in Phase W. Error bars: 95% confidence interval.

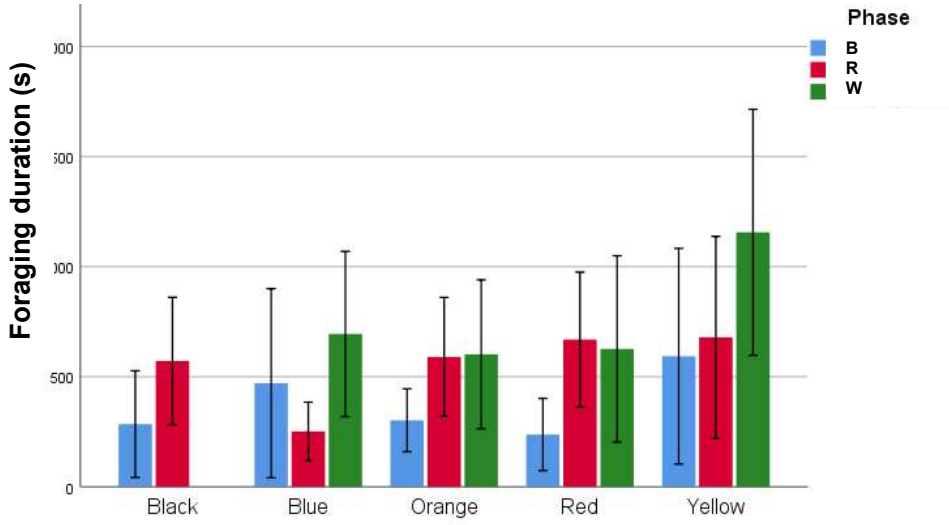



Figure 4.5 - Mean foraging duration across subjects during each experimental phase. Black did not participate in Phase W. Error bars: 95% confidence interval.

### 4.2.3 Discussion

Captive kea could forage from a tray containing objects that blocked food and from a tray with no added objects (i.e. free food). Kea contrafreeloaded as they foraged from a food tray requiring manipulation / removal of objects even when a second tray with food and no blocking objects was available.

#### 4.2.3.1 Baseline preferences

Baseline analyses of first chosen tray (FC) and duration of foraging behaviour (FD) showed no significant differences for choosing either tray first or foraging more from either tray.

#### 4.2.3.2 Do captive kea contrafreeload?

In Phase R, FC and FD did not significantly differ between trays, and similar results were found in Phase W. At the group level, FC and FD did not differ between trays. These results are considered evidence of contrafreeloading, as kea foraged at statistically similar levels from the two trays. This result differs from the findings of Rozek and Millam (2011) where Amazons only removed pellets from an open feeder, thus not contrafreeloading. However, Rozek and Millam's results were based on measuring the weight of food removed from the feeders, while the present experiment measured tray choices and foraging duration. Rozek and Millam discussed the possibility of previous experiments affecting the foraging behaviour of their subjects, as they had been exposed to three experiments with the same feeders but different pellet sizes, which could be considered as training, thus affecting contrafreeloading (Inglis et al., 1997).

As discussed in Chapter 1.3.6, the literature on contrafreeloading lists five explanations for this behaviour (Inglis et al., 1997): (1) operant dispensers might include stimuli that become secondary reinforcers, (2) training sessions could cue subjects' responses, (3) sensory reinforcement is caused by changes in earned food stimuli, (4) working for food involves uncertainty, exploration and ability self-assessment, which animals prefer, and (5) behaviour to obtain food acts as a reinforcement. As this study's protocols did not involve operant dispensers, training protocols, or modification of food characteristics, explanations 1, 2 and 3 are not relevant to these results.

Explanation 5 indicates that the behaviours performed while contrafreeloading could be reinforcing and thus the reason this phenomenon occurs. To obtain food from the trays with objects, kea were seen performing behaviours unique to this tray: moving, grabbing, lifting, and removing objects. These behaviours were observed in Phases W and R, thus

both phases would have been predicted to involve equal levels of contrafreeloading. Results (Figure 4.3) seemed to contradict this prediction as kea, overall, appeared to forage (non-significantly) more from the tray with objects during Phase W. Furthermore, Explanation 5 has been described as “unsatisfactory” (Inglis et al., 1997) to explain contrafreeloading. Gerbils (*Meriones unguiculatus*) given the choice to forage in two scenarios: 1) seeds in one bowl and seeds covered in sand in a second bowl, and 2) seeds in one bowl and only sand in a second bowl, were shown to contrafreeload via digging behaviour in Scenario 1 (Forkman, 1993). Digging behaviour was performed significantly less in Scenario 2, contradicting this contrafreeloading explanation, as digging was predicted to occur at similar levels in both scenarios if it were reinforcing. In the present study, kea also had the opportunity to engage in similar manipulation behaviours with other environmental items such as wood bark, sticks, soil, and even in the tray with no added objects as behaviours such as moving items around could also be performed in this tray, suggesting that FD should occur at similar levels in both trays, which was not the case.

Explanation 4 (a preference for uncertainty, exploration, or ability self-assessment) appears to partially explain the present findings. Uncertainty and self-assessment are not considered to be relevant factors in this experiment, as kea were receiving the same diet as usual and in the same locations. If the addition of rocks or wooden blocks involved uncertainty or a novel challenge involving self-assessment, the effect would be predicted to decrease over time, but it increased from Phase R to Phase W. Moreover, there is contradicting evidence in terms of contrafreeloading and uncertainty, as pigs have been shown to perform negligible contrafreeloading levels when being provided with free and uncertain food opportunities (based on fixed and variable operant schedules; Young and Lawrence, 2003).

#### 4.2.3.3 Enrichment implications

The relevance of this foraging manipulation as enrichment was assessed by two behaviours: foraging and object manipulation. In the wild, foraging behaviour occupies an important part of parrots’ daily activity budgets, as they often travel between different locations searching for food (e.g. Wirminghaus et al., 2001, Symes and Perrin, 2003) and “typically engage in a wide variety of foraging behaviours” that may dominate their daytime behaviours (Rozek and Millam, 2011; e. g. Francisco et al., 2002). In captivity, both locomotion and foraging behaviours are constrained, which, in turn, may negatively impact their well-being (Mason and Mendl, 1997; Rozek and Millam, 2011).

There were no significant differences in the duration of foraging behaviour across the study phases, indicating that, statistically, the addition of rocks and wooden blocks did not elicit any foraging effect. However, at the individual level, including wooden blocks and rocks in a food tray resulted in an increase of foraging duration in all but one kea. Furthermore, a two-fold increase in foraging duration was found in Phase W for two kea in comparison to Phase R (Figure 4.5), which agrees with the results of other studies on parrot enrichment (e.g. van Zeeland et al., 2013). One of the aims of foraging enrichment is “to encourage behaviours involved in food acquisition” (Fangmeier et al., 2019). Wild kea are extractive foragers with high exploration and destruction drives (Diamond and Bond, 1999). Phase W allowed for higher durations of specific foraging-related behaviours such as digging and manipulating objects to extract food in comparison to Phase R. Juvenile kea were even encouraged to engage in play-like behaviours when wooden blocks were provided.

Play behaviour is non-functional, different between juveniles and adults, and performed repeatedly and in the absence of threats (Burghardt’s, 2005). Play behaviour has also been discussed as an indicator of positive well-being (Held and Špinka, 2011). Play behaviour was performed by the three juvenile kea: they would manipulate wooden blocks with their feet and beaks, toss them, roll on their backs and hold the wooden blocks up and attempt to steal them between each other (Figure 4.6). Juvenile kea were not able to interact with rocks in the same way as wooden blocks as they were too heavy to be lifted.

Figure 4.6 – A juvenile kea interacting with an object from Phase W outside of the foraging context (i.e. playing).

The dataset for this experiment was unbalanced (i.e. different number of observations per treatment), which could be considered a methodological weakness. Unbalanced experiments are challenging when analysing treatment combinations (e.g. multiple multi-level factors, Milhken and Johnson, 1984), but since this study only involved one factor (Phase) with no combinations, design problems (e.g. statistical power and homoscedasticity) did not affect results (Milhken and Johnson, 1984).

Finally, these behavioural observations do not allow to perform a conclusive enrichment assessment, but they highlight how simple interventions such as adding objects to food trays instead of providing free-to-access food may allow the expression of behaviours associated with positive well-being.

### 4.4 Conclusions

- Kea did not show a significant positional preference towards either of two trays that were provided as their regular feeding husbandry during baseline analysis.

- Kea displayed a contrafreeloading response as they foraged from a food tray containing occluding items when an identical tray containing the same amount of food, but no occluding items was available.

- Adding rocks and wooden blocks to food trays did not have any significant effect in the expression of foraging and object manipulation behaviours but individual results and casual observations of play behaviour suggest a possible enriching effect that requires further research.

# Chapter 5. Effect of manipulanda and reward visibility on contrafreeloading

## Abstract

Contrafreeloading behaviour has been discussed as an indication that animals have a need to perform behaviours associated with working for a reward. Following this assumption, captive animals should receive opportunities to perform these behaviours in captivity. For this, there is a need to understand which work-related characteristics motivate captive animals to interact with them. Few studies have attempted to identify factors relevant to the contrafreeloading response, such as task difficulty and reward visibility. The literature on parrot enrichment has measured object-related variables that appeared to correlate with object interaction, such as material and colour. This “motivational” approach has not been studied in the context of contrafreeloading. This chapter presents an experiment determining task-related characteristics that motivate captive kea to contrafreeload. A wooden slab with ten holes allowed for ten rewards to be presented either with free access or covered by a manipulandum (lids, corks, and membranes). After being trained to operate manipulanda, kea were offered the board in one of the following setups: free versus obstructed visible pellets; free pellets versus obstructed, occluded pellets; visible versus occluded, obstructed pellets; and pairwise combinations of all manipulation types. Kea were found to contrafreeload, as they retrieved covered rewards in the presence of uncovered rewards, but they showed a preference to choose free pellets earlier in their ten-choice sequence. This response was stronger when kea could not see the food rewards. Kea also preferred membranes to corks and lids. Foraging and enrichment protocols can make us of these findings to deliver motivating opportunities, such as presenting visible rewards that are concealed by membrane-like materials.

## 5.1 Introduction

Chapter 4 showed that kea contrafreeloaded as they foraged from a tray including occluding objects while one without still contained food. In terms of time spent on each tray, kea had no preference to forage from either tray. Wooden blocks were associated with higher engagement based on observations of kea handling these objects more often than rocks. Results appeared conflicting as foraging duration was higher from the tray not containing rocks compared to the tray containing rocks, but foraging duration was higher from the tray with wooden blocks compared to the tray without them. This mismatch suggests that the type of occluding object may influence contrafreeloading.

Following the rationale that contrafreeloading indicates a need to perform certain behaviours (see Chapter 1.3.4) and the contrasting results of Chapter 4, it is of interest to determine which factors shape the contrafreeloading response in captive kea. Knowing these may help design tasks that captive kea will be motivated to interact with and, potentially, enhance their well-being. The contrafreeloading literature has attempted to identify key factors that affect the contrafreeloading response in captive animals. Table 1.1 presented a brief overview of contrafreeloading studies on captive animals; only four studies included in their methodologies variations of the work performed to determine effects on contrafreeloading (i.e. their methods went beyond providing free vs. non-free food and analysing which of these were favoured). These studies are discussed next.

Captive giraffes (*Giraffa camelopardalis*) were given foraging devices designed to increase foraging times based on oral manipulations with the objective of determining contrafreeloading preferences (free food was also available; Sasson-Yenor and Powell, 2019). Results indicated that some giraffes preferred to contrafreeload and some did not. Interestingly, contrafreeloading giraffes were found to choose the “more difficult” food source: difficulty was determined based on the length of giraffes’ tongue required to be inserted into the devices to retrieve food; higher difficulty required longer tongue length). Authors concluded that choosing to retrieve their preferred food via contrafreeloading is an indicator of the subjects’ need to perform foraging behaviours, as they could have followed an optimal foraging strategy and foraged from free food.

In another experiment, grizzly bears (*Ursus arctos horribilis*) were given apples or fish either as free-food or concealed inside a box or in ice (i.e. frozen food, McGowan et al., 2010). Empty boxes and ice not containing food were also simultaneously available to control for object-based reinforcement. Bears contrafreeloaded as they obtained and ate food from boxes and ice while free food was simultaneously present. In general, boxes were

manipulated more than ice, hinting that certain object-related contexts (e.g. required manipulation or food visibility) could affect the expression of contrafreeloading.

A study on gerbils (*Meriones unguiculatus*) investigated the effect of food availability and abundance on contrafreeloading (Forkman, 1996). Gerbils were tested in four different experiments with two food choices each: 1) seeds with husks and seeds without husk, 2) free-to-access seeds and seeds glued to a stick, 3) seeds in an uncovered bowl and one seed in multiple covered bowls, and 4) one tray with seeds and one tray with seeds, husks and sawdust. Analyses on the amount of seed eaten showed that gerbils preferred: 1) seed with husks, 2) free-to-access seed, 3) uncovered seeds (but a gradual, increasing preference to consume covered seeds was displayed), and 4) seeds from the tray with husks and sawdust. Forkman explained Results 1 and 2 based on both the optimal foraging model (Stephen and Krebs, 1986) as gerbils chose profitable food sources and the information primacy hypothesis (Inglis and Ferguson, 1986) as gerbils worked for information, not food, and contrafreeloading stopped when no new information was obtained. Forkman explained Results 3 and 4 only based on the information primacy hypothesis, as the optimal foraging theory predicted that the profitable choices would be preferred. Forkman discussed that gerbils preferred unprofitable food choices as these “contained more potentially new information”.

Following-up Forkman’s (1996) study, Bean and colleagues (1996) also studied the effect of food visibility on contrafreeloading behaviour on captive starlings (*Sturnus vulgaris*) by providing a dish with *ad libitum* turkey crumbs and a dish with a mixture of turkey crumbs and sand covered with an opaque membrane, or a dish with *ad libitum* turkey crumbs accompanied by a dish containing the previous mixture but covered with a transparent membrane. Data on the amount of food eaten showed that birds consumed more free food when transparent membranes covered the food and sand mix, interpreted as an effect on contrafreeloading from visual assessment of resources.

These four studies found contrafreeloading differences under different task-related variables. Briefly, these were: task difficulty based on oral manipulations (Sasson-Yenor and Powell, 2019), objects used to conceal food (McGowan et al., 2010), and food profitability and visibility (Forkman, 1996; Bean et al., 1996). However, there were some methodological aspects that could have confounded these results. For example, Sasson-Yenor and Powell (2019) tested giraffes in a group setting and, while the number of foraging devices was adapted to avoid monopolisation or competition, there was still is a social confound. Furthermore, a singly housed male giraffe was also tested and its data were pooled for analyses. In the experiment by McGowan and colleagues (2010), using either boxes or ice to

conceal food does not allow to identify specific characteristics that could elicit behavioural responses: their conclusions are only applicable to the specific tasks and elements used.

Chapter 4.1 discussed the three studies that have investigated contrafreeloading on parrots with contrasting results. The scope of these studies was only to determine if parrots contrafreeloaded but not to determine which variables influenced this response. The studies that have attempted to identify parrots' preferences towards tasks or resources come from the literature on psittacine enrichment. The preferences investigated by these studies corresponded to preferences towards auditory stimuli (Williams et al., 2017), foraging devices (van Zeeland et al., 2013), ultraviolet light (Ross et al., 2013), diet forms (Rozek et al., 2010; Rozek and Millam, 2011), and colours and materials (Webb et al., 2010). These preferences can be related to well-being via the "feelings" approach (motivations, see Chapter 1.2.2 and Chapter 6). Under the assumption that contrafreeloading species have a need to perform work-related behaviours, these preferences may be helpful in designing contrafreeloading opportunities, but research still must be conducted to determine if contrafreeloading indeed occurs.

As kea were found to contrafreeload in Chapter 4, the experiments in this Chapter investigate which task-related factors enhanced contrafreeloading following the research of Forkman (1996) and Bean et al. (1996). The over-arching objective of this study was to determine if contrafreeloading was performed *and* preferred under different manipulation and visibility contexts. For this, three experiments were developed where the manipulation required to obtain a food reward and reward visibility were modified, predicting that kea would contrafreeload across all contexts and show a contrafreeloading preference when rewards were uncertain (i.e. occluded).

In Experiment 1, kea could forage by manipulating transparent manipulanda. Its aims were to determine: 1) if kea contrafreeloaded by engaging in the foraging task, 2) if kea preferred to contrafreeload by analysing the exact order in which food rewards were retrieved, expecting all covered food rewards to be retrieved first as a preference indicator, 3) if type of manipulandum affected the contrafreeloading response by analysing the order of reward retrieval across manipulanda, and 4) if adding uncertainty to the foraging task via opaque manipulanda affected the contrafreeloading response. In Experiment 2, tests were repeated using transparent and opaque manipulanda simultaneously to determine if visual access to food rewards, independently from working to retrieve them, affected kea's responses. In other words, kea had a choice of working for visible and occluded rewards. In Experiment 3, comparisons were made between the three types of manipulanda to determine if kea had a manipulation preference.

## 5.2 Methods

This study was performed in two phases. Phase 1 (Experiment 1) happened between November 2017 and March 2018. Phase 2 (Experiments 2 and 3) was conducted between April and July 2018. The researcher entirely conducted phase 1 himself. Data from Phase 2 were collected by a visiting work experience student (Thirsa van Wichen) but the researcher still performed the corresponding analyses.

### 5.2.1 Study site

Research was undertaken at the Kea Lab at the Haidhlof Research Station in Bad Vöslau, Lower Austria (47.967°N, 16.144°E). The Haidlhof Research Station is a cooperative project between the University of Veterinary Medicine Vienna and the University of Vienna. The Haidlhof Research Station is not open to the public, but it organises a monthly tour to anyone interested in visiting the station.

### 5.2.2 Subjects and housing

At the time of the experiment, the Kea Lab housed 28 kea, a subset of this group was used for this study (Table 5.1). All kea were housed in an outdoor enclosure (520 $m^2$; Figure 5.1). The enclosure included two pools, wooden huts, plant beds, foraging tables, perching sites, rocks, wooden toys, see-saw, and tunnels. Small pebbles and sand were used as substrate. During the summer months, sprinklers provided bathing opportunities. Every compartment included a metallic bowl with water. Kea were fed three times per day. The first feed included a protein source (beef or eggs) and fruits or vegetables. The second and third feeds included fruits or vegetables and mixed seeds. In experiments where food rewards were used, preferred treats that were not part of the regular diet were used.

Table 5.1 – List of kea that participated in this study. All kea were captive born.

| Kea | Sex | Year born | Rearing[15] |
|---|---|---|---|
| Anu | Male | 2007 | Hand reared |
| Jean-Luc | Male | 2015 | Hand reared |
| John | Male | 1999 | Parent reared |
| Kermit | Male | 2004 | Hand reared |
| Lilly | Female | 2007 | Hand reared |
| Odo | Male | 2015 | Parent reared |

| Kea | Sex | Year born | Rearing |
|---|---|---|---|
| Papu | Female | 2013 | Hand reared |
| Paul | Male | 2010 | Parent reared |
| Pick | Male | 2004 | Hand reared |
| Plume | Female | 2007 | Hand reared |
| Roku | Male | 2008 | Parent reared |
| Sunny | Female | 2007 | Hand reared |
| Willy | Female | 207 | Hand reared |

[15] Hand-rearing (by human caretakers) and parent-rearing differentiation relevant as hand-reared and parent-reared parrots may behave differently (e.g. Schmid et al., 2006).

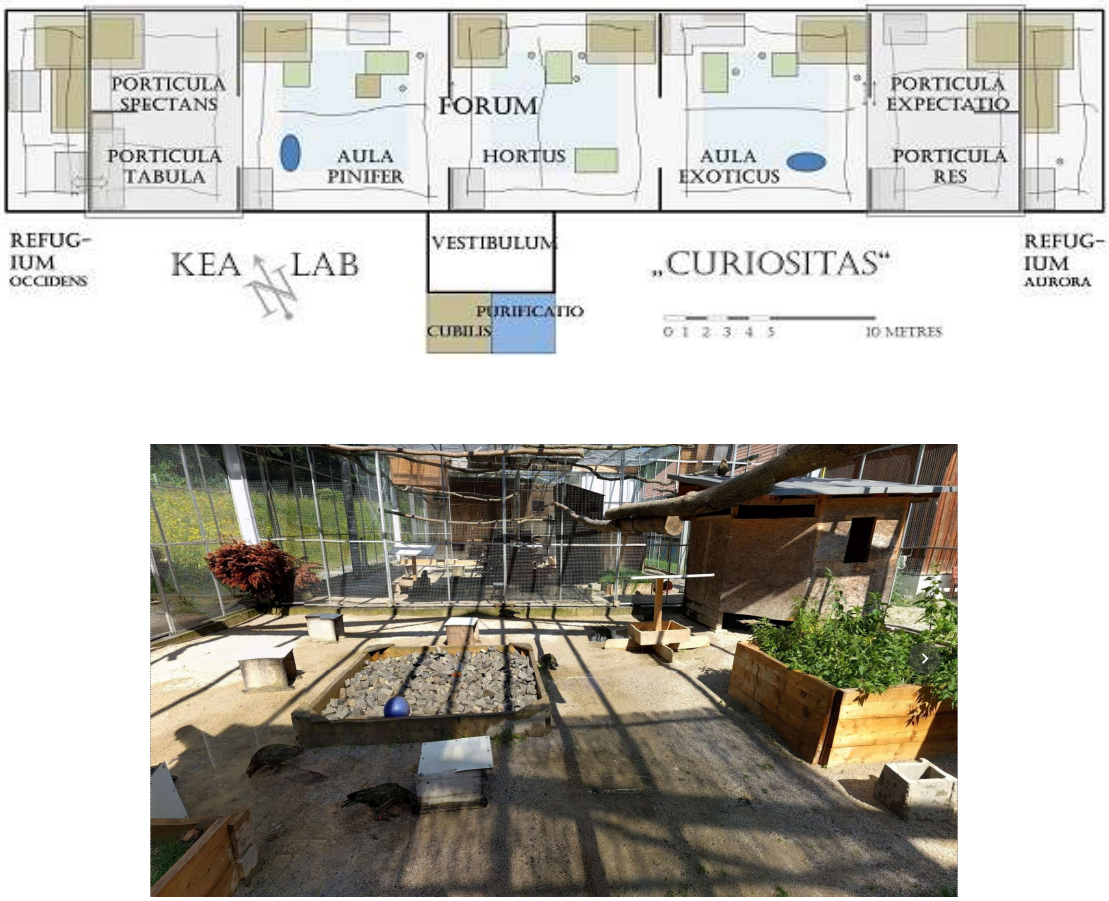



Figure 5.1 – Kea enclosure at the Kea Lab. Top: schematics. Protocols herein described were conducted in Porticula Spectans + Porticula Tabula. Bottom: inside view.

### 5.2.3 Apparatus and manipulanda

A foraging board was built by drilling ten 3 cm diameter holes onto a wooden slab (Figure 5.2). The board was screwed to a larger piece of wood to prevent kea from flipping the apparatus. Three different manipulanda were constructed to cover holes. The first was a rotatable lid made from acrylic and attached (Experiment 1A). The second was a “pseudo-cork” made from acrylic and a bolt and nut inserted through it (Experiment 1B). The third was a membrane stapled over the holes (Experiment 1C). Each manipulandum included ten items (one per hole) and had an opaque and a transparent version (white and transparent acrylic for lids and corks, white paper, and transparent cellophane for membranes).

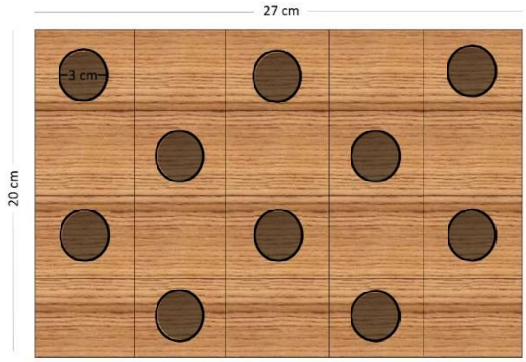



Figure 5.2 - Foraging board dimensions. Dark circles represent the holes in which food rewards were placed.

### 5.2.4 Experimental protocols

During experimental sessions, kea were either called or brought into the experimental compartment on the experimenter's arm; kea could choose not to enter the compartment and not participate in testing. Sessions occurred between feeding times. All tests were performed with subjects visually isolated from conspecifics by opaque sliding doors. One half of the compartment served as a waiting room for the subject while the experimenter set up the apparatus. A test started when the sliding mesh of the waiting room was opened and ended when the kea obtained the last food reward. All sessions were video recorded. For Experiments 1A and 1B, training sessions were performed to ensure kea were able to use the manipulanda as expected and allow conclusions based on manipulandum type as a variable as if kea interacted with manipulanda differently (e.g. breaking or rotating lids) conclusions could be confounded by this manipulation difference. Also, training allowed to verify that the foraging task was solvable.

#### 5.2.4.1 Experiment 1A – Do kea (prefer to) contrafreeload in a foraging task by rotating transparent lids?

Ten plastic, transparent lids were screwed onto the foraging board. Holes could be uncovered by rotating the lids. In the initial training phase, all ten holes contained a food reward. Five random holes had lids covering the reward and the other five were uncovered. During a training session, kea could freely manipulate the foraging board until all food items were obtained. Subjects were considered trained when they recovered all food items correctly (i.e. obtaining covered pellets by rotating the lid instead of breaking them or thrashing the board) during a session. After training, the time needed to retrieve pellets when all holes were covered or uncovered was measured as an indicator of task difficulty. All holes were covered or uncovered and only five contained a reward to test if kea showed interest in non-baited holes to determine if transparent lids were not perceived as

transparent or the manipulandum involved intrinsic reinforcement. If kea did not perceive lids as transparent or if lids were reinforcing, manipulation of all ten options in the covered setup was predicted. Each kea received six sessions: three with holes covered and three with holes uncovered. Finally, kea received six sessions with all holes containing a pellet, half of them covered and five uncovered (holes covered/uncovered randomised across sessions). These six sessions will be referred to hereafter as “main testing phase”.

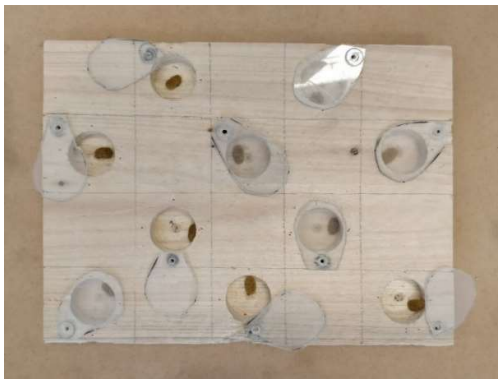


Figure 5.3 – Training setup for Experiment 1A.

#### 5.2.4.2 Experiment 1B – Do kea (prefer to) contrafreeload in a foraging task with different transparent manipulanda?

Lids from Experiment 1A were replaced with membranes and corks (Figure 5.4). Circular pieces of cellophane were used as transparent membranes; to cover holes, membranes were stapled onto the board. Corks were acrylic circles with a bolt and nut screwed onto them and placed in holes. Kea had to grab these manipulanda and remove them to access pellets. No training occurred with these manipulanda. As in Experiment 1A, the time needed to retrieve pellets when all holes were covered or uncovered was measured as an indicator of task difficulty for each manipulandum. The same protocol was followed for membranes and corks apart from them being scattered over the board to see if kea manipulated them and control for intrinsic reinforcement. Finally, kea received six sessions for each manipulandum in which all ten holes had a pellet, five were covered and five were uncovered (main testing phase). During Experiment 1B, sessions for each manipulandum were counterbalanced so that half of the kea were tested first with the lids and then with membranes and vice versa.

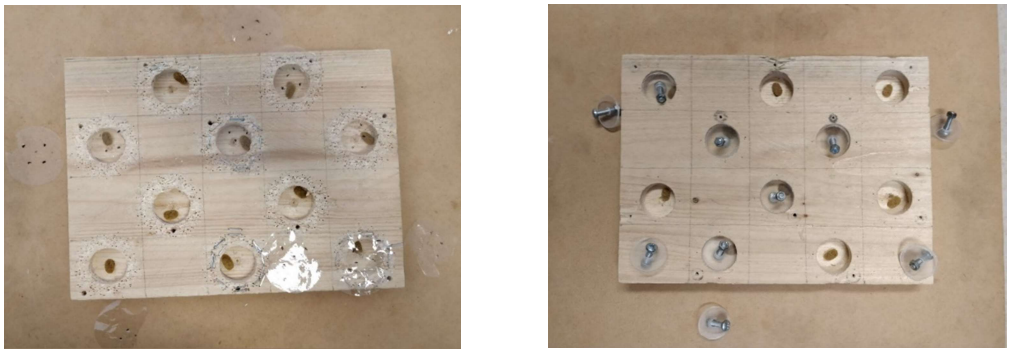


Figure 5.4 Foraging board appearance in Experiment 1B. Left: transparent membranes. Right: transparent corks.

#### 5.2.4.3 Experiment 1C – Do kea (prefer to) contrafreeload in a foraging task when the non-free food is occluded?

Manipulanda from Experiments 1A and 1B were replaced with opaque versions to determine kea's responses when they could not see hole contents (Figure 5.5). Opaque lids and corks were made of white plastic and membranes of white paper. Kea were not trained with opaque manipulanda nor received sessions to determine time needed to retrieve pellets. Kea received six sessions per manipulandum where all holes had a pellet, half of them covered and half uncovered. To maintain consistency with experiments 1A and 1B, kea first received six sessions with opaque lids and then twelve sessions with corks and membranes, counterbalanced between individuals.

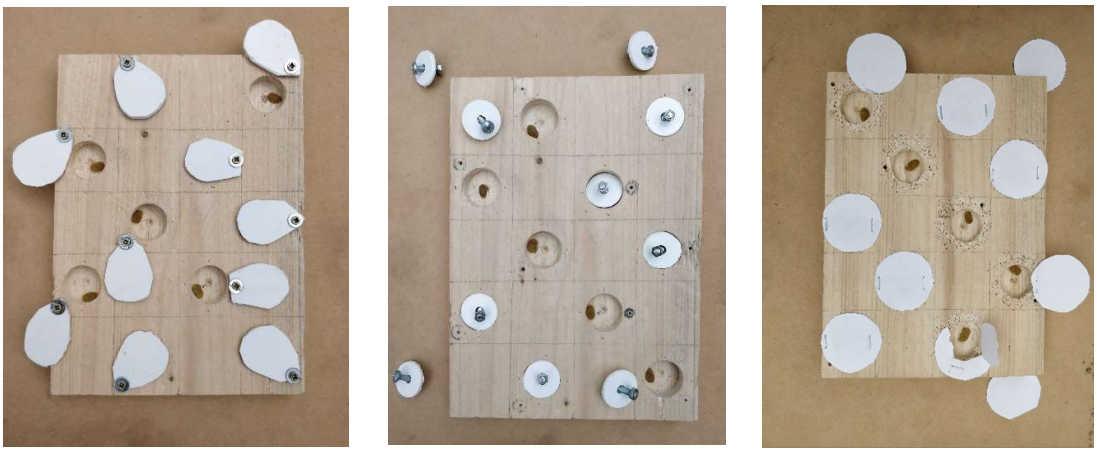


Figure 5.5 – Foraging boards with opaque manipulanda. Left: lids, centre: corks, right: membranes.

#### 5.2.4.4 Experiment 2 – Foraging preferences in terms of reward visibility

For each manipulandum type, kea received six sessions with all holes including a pellet and covered, half by a transparent manipulandum and half by its opaque version. The order in which subjects received a session of each manipulandum type was randomised between the three manipulation types.

#### 5.2.4.5 Experiment 3 – Manipulandum preferences

The foraging board was provided with two manipulanda of the same opacity (opaque membrane - opaque lids, opaque membranes - opaque corks, opaque lids - opaque corks, transparent membrane – transparent corks, transparent membranes – transparent lids, transparent corks – transparent lids). All holes contained a pellet and were covered, five by one manipulandum type and five by its pairing. Six sessions were carried for each combination.

### 5.2.5 Behaviour coding and analysis

All sessions were video recorded. Videos were analysed using The Observer XT10 (Noldus) to obtain: behaviours pertaining to solving the foraging task (Table 5.2), the exact order in which pellets were retrieved, and if a choice was an uncovered or covered hole. Holes were assigned a number from 1-10, choices were numbered accordingly and assigned a yes/no value if they had chosen, or not, a covered hole in Experiments 1A, 1B and 1C or a transparent manipulandum in Experiment 2. In Experiment 3, chosen manipulandum was registered as a nominal variable (lids, corks, or membranes). Since kea received multiple sessions for a given treatment, data for each treatment's sessions were aggregated by calculating proportions. For example, in Experiment 1A each kea received six sessions with transparent lids, half covered and half uncovered. A proportion of covered holes accessed was calculated per individual and per session. For example, if a kea chose a covered hole in their first choice in all sessions, they would get a "summary" proportion of 1 for that first choice.

To verify if covered holes required more work than uncovered holes, paired T-tests were performed with manipulation time (MT) of each condition in Experiments 1A and 1B. Linear regressions were performed with the data for all kea, using choice order sequence as a predictor for the proportion of covered / uncovered choices in Experiments 1A, 1B and 1C. If kea preferred to contrafreeload, the regression would show a negative correlation between these variables (i.e. higher proportion of covered holes in earlier choices). As linear regressions do not allow investigation of the dependent variable (proportion of closed holes) at the different levels of the independent variable (choice order), one and two-way repeated

ANOVAs were conducted to determine if there were significant differences between the proportion of covered holes across the ten choices. The factors for these ANOVAs were choice order for Experiments 1A, and choice order and manipulation type for Experiments 1B and 1C. Regressions and repeated ANOVAs were performed with data from Experiments 2 and 3 to determine if kea showed a preference for uncertainty (i.e. not being able to see the reward due to opaque manipulanda) and for a type of manipulandum. Only data from experiments with a counterbalanced design were grouped for statistical analyses.

The two-way repeated ANOVAs in Experiments 1B, 1C, and 2 were found to be non-normally distributed. To deal with this normality violation, two analyses were performed: 1) the original two-way repeated ANOVA, as there is no equivalent non-parametric test, is considered robust against non-normal data (Laerd Statistics, 2015), and deals appropriately with the experimental design (treating manipulandum type and choice number as factors), and 2) non-parametric (Friedman) tests, one for each manipulandum. All statistical analyses were performed using IBM SPSS Statistics 24.

Table 5.2 – Behaviours coded to determine the difficulty contrast between covered and uncovered holes.

| Behaviour | Description |
|---|---|
| Object interaction (OI) | Kea interacting with manipulandum by grabbing, pushing, lifting, holding; interactions directed towards non-futile manipulanda (i.e. manipulandum that cover access to a food reward). |
| Futile[16] object interaction (FOI) | As per OI but manipulating a futile manipulandum (i.e. it is not covering access to a food reward). |
| Pellet retrieval (PR) | State behaviour commencing when a kea placed its beak in an uncovered hole (containing a food reward) and ended when the food reward was taken out of the hole. |
| Manipulation time (MT) | Behavioural category calculated by adding OI and PR. |

## 5.3 Results

### 5.3.1 Experiment 1A – Do kea (prefer to) contrafreeload in a foraging task by rotating transparent lids?

#### 5.3.1.1 Training

Eight kea opened the lids by rotating them in the first training session and were not trained further. The other five tried to lift or thrash the board to gain access to the pellets. Of these five kea, two properly rotated lids and stopped thrashing the board by the second

[16] "Futile" described a manipulation not resulting in retrieving of a food reward. It did not imply that the manipulation or other behaviours did not have another cryptic function.

training session and were not trained further. The remaining kea required an additional session to retrieve the pellets just by rotating the lids.

### 5.3.1.2 Difficulty contrast between covered and uncovered holes

Four kea manipulated lids not covering a reward (i.e. futile lids). Three kea manipulated futile lids in six sessions from the covered treatment and one kea manipulated futile lids in one session of the uncovered treatment. FOI duration of holes covered by lids had a range of (1.24, 6.08) s. Mean MT for covered and uncovered holes was calculated for each kea. No outliers were found via inspection of the difference boxplot. Differences between covered and uncovered MT were normally distributed (Shapiro-Wilk's test, $W_{13}$=0.920, p=0.251). Data are presented as mean ± standard deviation unless otherwise stated. Kea took significantly longer (paired t-test, $t_{12}$=10.3, p<0.0005) to obtain pellets when lids covered holes (22.5 ± 6.2 s) as opposed to uncovered holes (3.5 ± 1.2 s; Figure 5.6). Covering holes with lids significantly increased MT by 18.9 s (95% CI, 14.8 to 22.9).

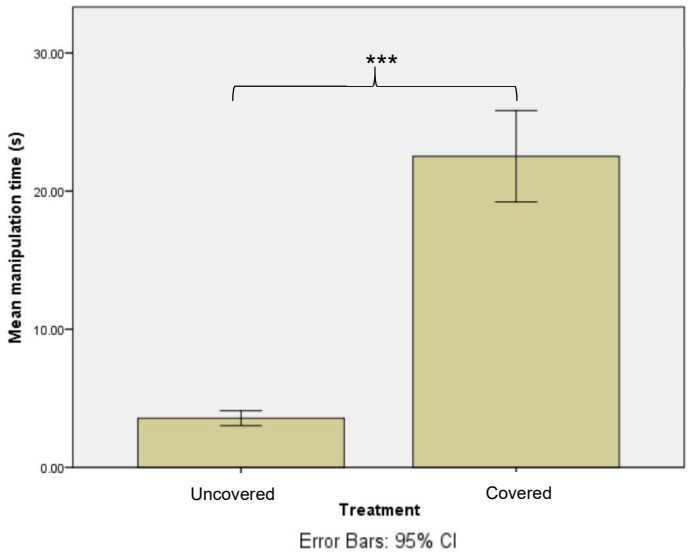



Figure 5.6 – Mean Manipulation Time for covered and uncovered holes using transparent lids (Experiment 1A, N=13 kea). *** indicates significance at the p<0.001 level.

### 5.3.1.3 Main testing phase

The main testing phase (food reward in all holes, half covered and half uncovered) comprised 78 sessions (six per individual). However, three sessions (each one from a different kea) had to be removed from statistical analyses because the researcher made a mistake during the setup process, failing to provide five covered and five uncovered holes, leaving a total of 75 sessions. The regression model showed independence of residuals (Durbin-Watson statistic of 1.972, Laerd Statistics, 2015). One outlier (one case with a

proportion of covered holes of 1, meaning all subjects chose a covered hole) was found and kept in the analysis after repeating the regression analysis without the outlier and finding similar results (with outlier: p<0.001, 95% confidence interval 0.081–0.104; without outlier: p<0.001, 95% confidence interval 0.083–0.105; Laerd Statistics, 2015). There was homoscedasticity, as assessed by visual inspection of a plot of standardized residuals versus standardized predicted values. Residuals were normally distributed as assessed by visual inspection of a normal probability plot. Choice number accounted for 66% of the variation in the proportion of covered holes with adjusted $R^2$= 65.7%. Choice number significantly predicted the proportion of covered holes, $F(1, 128)=248.4$, $p<0.001$. The regression equation was predicted proportion of covered holes=-0.011+0.093x(choice number). Figure 5.7 presents mean proportion of covered holes accessed across choices. The proportion of covered holes was found to be significantly different at the different choices ($F_{9, 108}=25.036$, $p<0.001$). Pairwise comparisons showed significant differences between choices 1-5, 1-6, 1-7, 1-8, 1-9, 1-10, 2-5, 2-6, 2-7, 2-8, 2-9, 2-10, 3-9, 3-10, 4-9, 4-10, 5-9, 5-10, 6-9, 6-10 and 7-10. Appendix 3 shows all statistical parameters for pairwise comparisons.

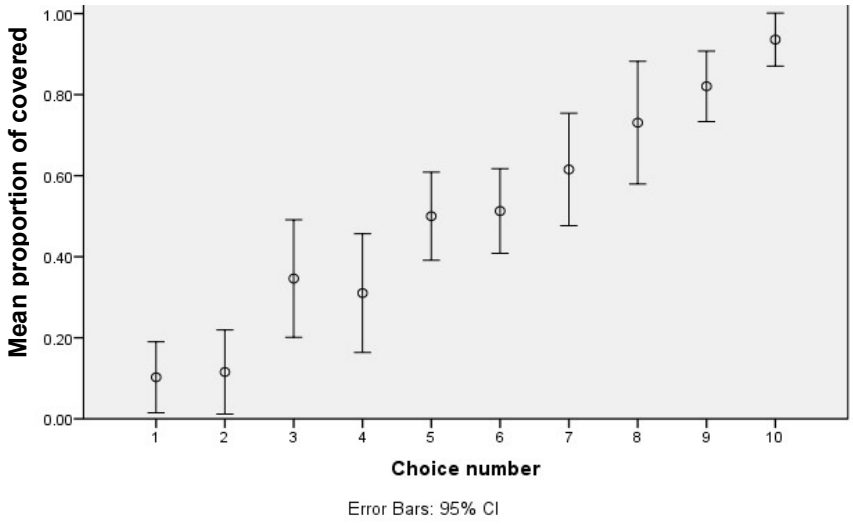



Figure 5.7 - Mean proportion of covered holes accessed for each choice number (N=13 kea). See text for choice-number pairs with significant differences.

### 5.3.2 Experiment 1B – Do kea (prefer to) contrafreeload in a foraging task with different transparent manipulanda?

#### 5.3.2.1 Difficulty contrast between covered and uncovered holes

Most kea were observed manipulating futile membranes and corks (i.e. manipulanda not covering a reward), only one kea never manipulated futile corks. Three kea manipulated

futile corks in the covered phase (i.e. after being removed from the holes). Five kea manipulated futile membranes in both conditions (uncovered and covered holes). One kea manipulated futile transparent membranes once during the covered-holes condition. One kea manipulated futile transparent membranes once during the uncovered-holes condition. The duration of cork FOI when holes were covered had a range of (0.4, 11.48) s. The duration of cork FOI when holes were uncovered had a range of (0.24, 1.24) s. The duration of transparent membrane FOI when holes were covered had a range of (1.72, 20.38) s. The duration of transparent membrane FOI when holes were uncovered had a range of (0.4, 29.44) s.

A paired t-test was planned to compare MT between covered and uncovered transparent membrane phases MT differences were not normally distributed (Shapiro-Wilk's test, $W_{39}$=0.937, p=0.030). Attempts at transforming data were made but data still showed a non-normal distribution thus a Wilcoxon's signed-rank test was performed instead. Kea took longer to obtain pellets when transparent membranes covered holes (median: 19.34 s) as opposed to non-covered holes (median: 3.3 s). Covering holes with transparent membranes caused an increase of 14.3 (95% CI, 11.3 to 17.3) s in MT. Holes covered with transparent membranes caused a significant increase in MT when compared to uncovered holes, z=-3.18, p=0.001.

A paired t-test was run to compare MT between covered and uncovered transparent cork phases. Two non-extreme outliers were identified but they were kept in the analysis. MT differences between covered and uncovered holes were not normally distributed (Shapiro-Wilk's test, $W_{39}$=0.926, p=0.013). Data were square-root-transformed and differences were now found to be normally distributed ($W_{39}$=0.976, p=0.571). MT was higher when retrieving pellets from holes covered with corks (19.7 ± 7.45 s) as opposed to uncovered holes (6.0 ± 3.7 s). Covering holes with corks caused a mean increase of 13.7 (95% CI, 8.9 to 18.6 s). Covering pellets with corks elicited a significant increase in MT when compared to uncovered holes, $t_{12}$=6.177, p<0.001. Figure 5.8 shows MT data during the six baseline sessions for each treatment.

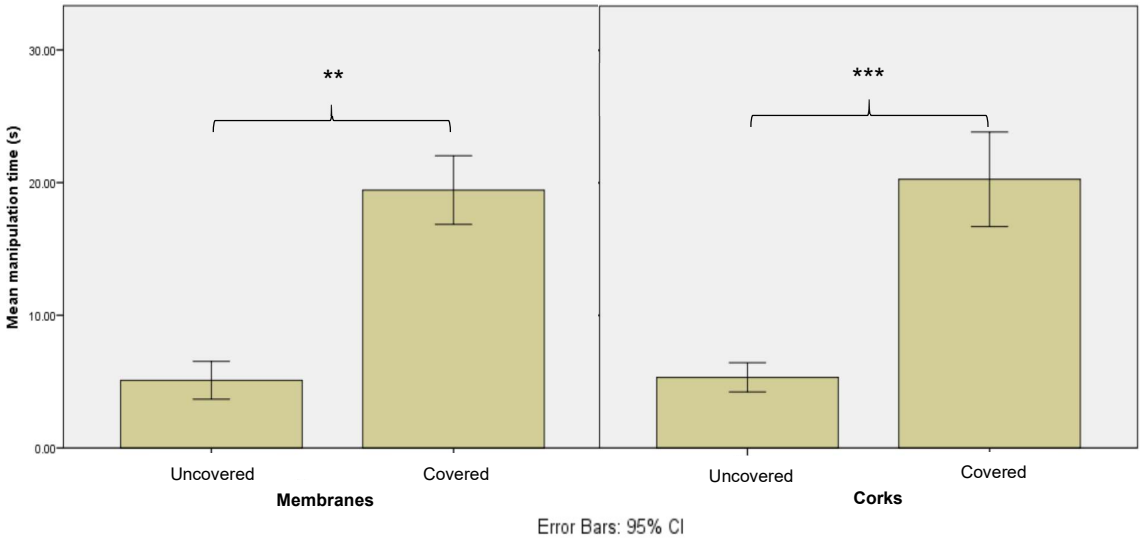



Figure 5.8 - Mean Manipulation Time when pellets were covered by membranes (left) and corks (right). ** indicates significance at the p<0.001 level, *** indicates significance at the p<0.0001 level. MT data for corks are shown non-transformed.

### 5.3.2.2 Main testing phase

The main testing phase comprised 74 sessions for membranes and 78 sessions for corks. This difference in the number of sessions was due to a lack of interest from one kea to be tested in the membrane treatment.

A multiple linear regression was performed including order sequence (1-10) and type of manipulandum (membrane or cork) as predicting variables and the proportion of covered holes as the predicted variable. There was linearity as assessed by partial regression plots and a plot of studentized residuals against the predicted values. There was independence of residuals, as assessed by a Durbin-Watson statistic of 1.882. There was homoscedasticity, as assessed by visual inspection of a plot of studentized residuals versus unstandardized predicted values. There was no evidence of multicollinearity, as assessed by tolerance values greater than 0.1. There were no studentised deleted residuals greater than ±3 standard deviations, no leverage values greater than 0.2, and values for Cook's distance above 1. The assumption of normality was met, as assessed by a Q-Q Plot. The regression significantly predicted the proportion of covered holes ($F_{2, 257}$= 34.573, p<0.001, adjusted $R^2$=0.206; Table 5.3) with Choice order being a significant predictor of Proportion of covered holes (p<0.001).

Table 5.3 - Parameters of the regression predicting proportion of covered holes with choice order and manipulandum type.

| | Unstandardized Coefficients | | Standardized Coefficients | | |
|---|---|---|---|---|---|
| | **B** | **Std. Error** | **Beta** | **t** | **p** |
| Constant | 0.285 | 0.052 | | 5.442 | <0.001 |
| Manipulandum | -0.004 | 0.028 | -0.007 | -0.127 | 0.899 |
| Choice order | 0.041 | 0.005 | 0.460 | 8.314 | <0.001 |

A two-way repeated measures ANOVA was performed with the proportion of covered holes across the ten choices and the two manipulanda (Figure 5.9). There were no outliers, as assessed by examination of studentised residuals for values greater than ±3 (Laerd Statistics, 2015). Assessment of the normality of proportion of covered holes was performed via Shapiro-Wilk tests on the studentised residuals (determined by p>0.05). The following data points did not show a normal distribution: Choice 3 with Corks ($W_{13}$=0.853, p=0.031), Choice 9 with Corks ($W_{13}$=0.865, p=0.045), Choice 4 with Transparent membrane ($W_{13}$=0.782, p=0.004), Choice 6 with Transparent membrane ($W_{13}$=0.835, p=0.019), and Choice 10 with Transparent membrane ($W_{13}$=0.818, p=0.011). Data were square root transformed but residuals still violated normality (logarithmic and reciprocal transformations were not performed as some data points had a value of zero and resulted in undefined transformations). As discussed in Section 5.2.5, the two-way repeated ANOVA was still calculated in addition to two Friedman tests, one for membranes and one for corks.

For the two-way repeated ANOVA, Mauchly's test indicated that the assumption of sphericity was met for the two-way interaction, $\chi 2(44)=50.711$, p=0.321. There was a statistically significant two-way interaction between manipulandum type and choice order ($F_{9, 108}$ = 3.558, $p$=0.001). Inspection of the Estimated Marginal Means Profile Plot corroborated that the proportion of covered holes had a different relationship (positive or negative) depending on both Choice order and Manipulation type, as described by the significant two-way interaction. This effect was more pronounced during Choices 1 – 5, as in choices 5 – 10 the Profile Plots were almost parallel (parallelism is a possible indicator for significant interactions; Laerd Statistics, 2015). Choice order had a significant effect on the proportion of covered holes ($F_{9, 108}$=9.290, p<0.001). Type of manipulandum did not have a significant effect on the proportion of covered holes ($F_{9, 108}$=0.262, p=0.618). Pairwise comparisons showed significant differences in choices 1-2, 1-6, 1-7, 1-8, 1-9, 1-10, 2-5, 2-6, 3-10, 4-10, 5-10 and 7-10. Appendix 3 shows all statistical parameters for pairwise comparisons.

The Friedman test for transparent corks showed that the proportion of covered rewards accessed was significantly different across the ten choices ($\chi^2_9$= 54.622, p<0.0001). Pairwise comparisons with a Bonferroni correction showed significant differences in the following choices: 1-6, 1-8, 1-9, 1-10, 3-9, 3-10, 5-10. The Friedman test for transparent membranes showed that the proportion of covered rewards accessed was significantly different across the ten choices ($\chi^2_9$= 28.840 p=0.001). Pairwise comparisons with a Bonferroni correction showed significant differences in the following choices: 1-4, 1-10, 5-10.

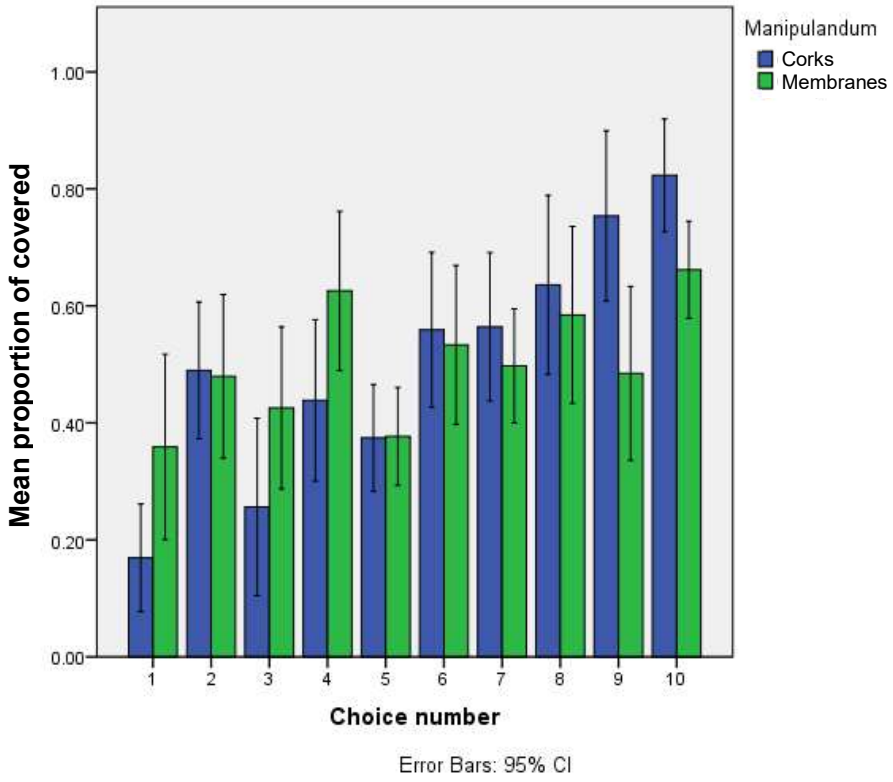



Figure 5.9 - Mean proportion of covered holes accessed in each choice of the 10-choice sequence with transparent corks and membranes. Mean values calculated across kea (N=13) and sessions (6). See text for significant choice-numbers pairs.

### 5.3.3 Experiment 1C – Do kea (prefer to) contrafreeload in a foraging task when non-free food is occluded?

The opaque lids phase comprised 67 sessions. One kea was not tested in this phase and another kea was tested only in four sessions because they were isolated for breeding purposes. Another kea did not complete three sessions as she stopped interacting with the foraging board.

The linear regression model predicting proportion of covered holes with choice number showed independence of residuals, as assessed by a Durbin-Watson statistic of 1.628. No outliers were found. There was homoscedasticity, as assessed by visual inspection of a plot of standardized residuals versus standardized predicted values. Residuals were normally distributed as assessed by visual inspection of a normal probability plot. Choice number accounted for 79.7% of the variation in the proportion of covered holes with adjusted $R^2$= 79.5%. Choice number significantly predicted the proportion of covered holes, $F_{1, 118}$ =463.3, $p$<0.001. The regression equation was: predicted proportion of covered holes = -0.244 + 0.134 x (choice number). Figure 5.10 shows mean proportion of covered holes across choices.

A one-way repeated ANOVA was conducted to determine if there were significant differences between the proportion of covered holes across the ten choices (Figure 5.10). Proportion of covered holes was statistically significantly different across choices order ($F_{9, 99}$=94.6, $p$<0.001). Pairwise comparisons showed significant differences in choices 1-5, 1-6, 1-7, 1-8, 1-9, 1-10, 2-5, 2-6, 2-7, 2-8, 2-9, 2-10, 3-5, 3-6, 3-7, 3-8, 3-9, 3-10, 4-6, 4-7, 4-8, 4-9, 4-10, 5-6, 5-7, 5-8, 5-9, 5-10, 6-8, 6-9, 6-10 and 9-10. Appendix 3 shows all statistical parameters for pairwise comparisons.

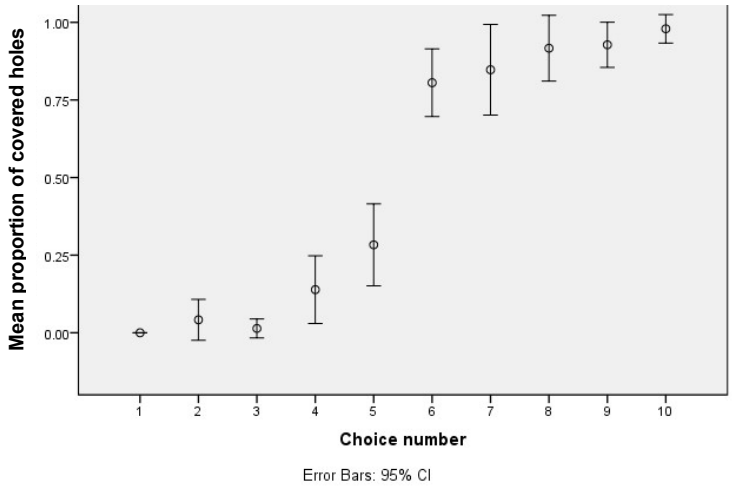



Figure 5.10 - Mean proportion of covered holes for each choice number calculated for all kea (N=13) and sessions. See text for choice number pairs with significant differences.

A multiple linear regression was performed including order sequence (1-10) and manipulandum type (opaque membrane or opaque cork) as predicting variables and the proportion of covered holes as the predicted variable. There was linearity as assessed by partial regression plots and a plot of studentized residuals against the predicted values. There was independence of residuals, as assessed by a Durbin-Watson statistic of 1.595.

There was homoscedasticity, as assessed by visual inspection of a plot of studentized residuals versus unstandardized predicted values. There was no evidence of multicollinearity, as assessed by tolerance values greater than 0.1. There were no studentised deleted residuals greater than ±3 standard deviations, no leverage values greater than 0.2, and values for Cook's distance above 1. The assumption of normality was met, as assessed by visual inspection of the Q-Q Plot. The regression significantly predicted the proportion of covered holes, $F_{2, 237}$=211.7, p<0.001, adjusted $R^2$=0.640. Only Choice number was a significant predictor of the proportion of covered holes (p<0.001). The regression coefficients' statistics can be found in Table 5.4.

Table 5.4 - Regression coefficients for the model predicting proportion of covered holes.

| | Unstandardized Coefficients | | Standardized Coefficients | | |
|---|---|---|---|---|---|
| | **B** | **Std. Error** | **Beta** | **t** | **P** |
| Constant | -0.108 | 0.056 | | -1.939 | 0.054 |
| Manipulandum | 0.010 | 0.030 | 0.013 | 0.337 | 0.736 |
| Choice number | 0.109 | 0.005 | 0.802 | 20.570 | <0.001 |

A two-way repeated ANOVA was calculated with the proportion of covered holes across the ten choices and the two manipulanda (Figure 5.11). There were no outliers, as assessed by examination of studentised residuals for values greater than ±3 (Laerd Statistics, 2015). Choice 2 with Corks ($W_{10}$=0.750, p=0.039), Choice 3 with Corks ($W_{10}$=0.779, p=0.008), Choice 8 with Corks (p=0.001), Choice 2 with Membrane (p<0.001), Choice 3 with Membrane (p=0.006), Choice 4 with Membrane (p=0.004), Choice 6 with Membrane (p=0.027), Choice 7 with Membrane (p=0.002), Choice 8 with Membrane (p=0.001), Choice 9 with Membrane (p<0.001), and Choice 10 with Membrane (p<0.001) did not have a normal distribution, as assessed by Shapiro-Wilk's test of normality on the studentized residuals. As explained in Section 5.2.5, the two-way repeated ANOVA was still performed in addition to two Friedman tests. Mauchly's test of sphericity indicated that the assumption of sphericity was not met for the two-way interaction ($\chi^2_{44}$=92.405, p<0.001). Greenhouse-Geisser corrections were used since ε=0.347 (Maxwell and Delaney, 2004). There was a significant two-way interaction between manipulandum type and choice order, ($F_{3.119, 31.189}$=1.846, $p$=0.001). Choice order had a significant effect on Proportion of covered holes ($F_{9, 90}$=38.892, p<0.001). Type of manipulandum did not have a significant effect on proportion of covered holes ($F_{1, 10}$=1.889, p=0.199). Pairwise comparisons showed significant differences in choices 1-5, 1-6, 1-7, 1-8, 1-9, 1-10, 2-6, 2-8, 2-9, 2-10, 3-6, 3-7, 3-8, 3-9, 3-10, 4-8, 4-9, 4-10, 5-8, 5-9, 5-10, 6-9 and 6-10. Appendix 3 shows statistical parameters for pairwise comparisons.

The Friedman test for corks showed that the proportion of opaque corks accessed was significantly different across the ten choices ($\chi^2_9$=64.737, p<0.001). Pairwise comparisons with Bonferroni corrections showed significant differences in the following choices: 1-7, 1.8, 1-9, 1.10, 2-8, 2-9, 2-10, 3-8, 3-10, 4-10. The Friedman test for opaque membranes showed significant differences across the ten choices ($\chi^2_9$=80.554, p<0.0001). Pairwise comparisons with Bonferroni corrections showed significant differences in the following choices: 1-6, 1-7, 1-8, 1-9, 1-10, 2-8, 2-9, 2-10, 3-8, 3-9, 3-10, 4-8, 4-9, 4-10, 5-10. Appendix 3 shows the full statistic parameters of the pairwise comparisons.

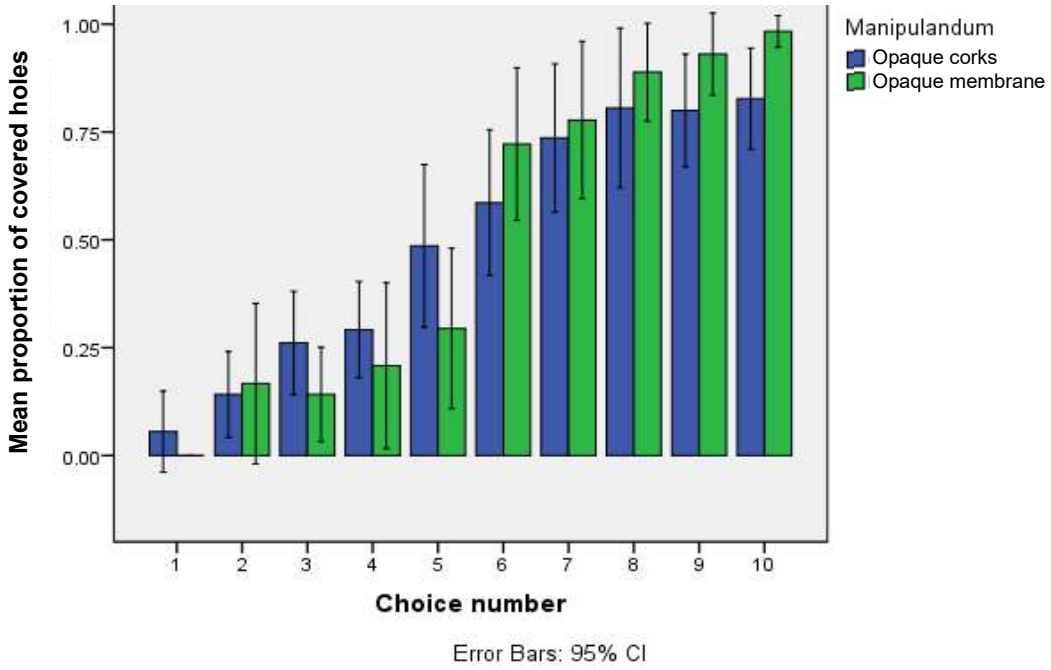



Figure 5.11 - Mean proportion of covered holes accessed during each choice in the 10-choice sequence with corks and membranes. See text for significant choice-numbers pairs.

### 5.3.4 Experiment 2 – Foraging preferences in terms of reward visibility

Up to six sessions per kea were carried comparing the transparent and opaque version of each of the three manipulandum types.

The linear regression predicting the proportion of opaque manipulandum choices (against transparent choices) with manipulandum type and choice order showed independence of residuals, as assessed by a Durbin-Watson statistic of 1.711. There was homoscedasticity, as assessed by visual inspection of a plot of studentised residuals versus unstandardized predicted values. There was no evidence of multicollinearity, as assessed by tolerance values greater than 0.1. There were no studentised deleted residuals greater than

±3 standard deviations, no leverage values greater than 0.2, and values for Cook's distance above 1. The assumption of normality was met, as assessed by a Q-Q Plot. The regression significantly predicted the proportion of opaque holes accessed, F(2, 217)=28.657, p<0.001, adjusted $R^2$=0.202. Only Choice order was a significant predictor of Proportion of opaque holes (p<0.001). Regression coefficients' statistics can be found in Table 5.5.

Table 5.5 - Regression coefficients for the model predicting proportion of covered holes accessed.

| | **Unstandardized Coefficients** | | **Standardized Coefficients** | **t** | **P** |
|---|---|---|---|---|---|
| | **B** | **Std. Error** | **Beta** | | |
| Constant | 0.286 | 0.050 | | 5.690 | <0.001 |
| Manipulandum | -0.001 | 0.019 | -0.004 | -0.069 | 0.945 |
| Choice number | 0.040 | 0.005 | 0.457 | 7.570 | <0.001 |

A two-way repeated ANOVA was calculated with the proportion of holes covered with opaque manipulanda across the ten choices and the three manipulandum types (Figure 5.12). There were no outliers, as assessed by examination of studentised residuals for values greater than ±3. Proportion of covered holes was normally distributed ($p$>0.05) except for Choice 1 with Lids (p=0.004), Choice 2 with Corks (p=0.004), Choice 3 with Corks (p=0.008), Choice 1 with Membrane (p=0.001), Choice 3 with Membrane (p=0.038), Choice 4 with Membrane (p=0.032), Choice 9 with Membrane (p=0.028) and Choice 10 with Membrane (p=0.008) as assessed by Shapiro-Wilk's test of normality on the studentized residuals. As explained in Section 5.2.5, the two-way repeated ANOVA was still performed in addition to three Friedman tests. The two-way repeated measures ANOVA showed a significant two-way interaction between manipulandum type and choice order, ($F_{18, 162}$=3.939, $p$<0.001). The main effect of manipulation type showed a statistically significant difference in the proportion of opaque manipulanda accessed between choices ($F_{2,18}$=4.554, $p$=0.025). The main effect of choice number showed a statistically significant difference in the proportion of opaque manipulanda accessed between choices, ($F_{9, 81}$=10.086, p<0.001). Pairwise comparisons did not show significant differences between manipulandum types. Pairwise comparisons showed significant differences in choices 1-9, 1-10, 2-9, 2-10, 4-9 and 4-10. Appendix 3 shows all statistical parameters for pairwise comparisons.

The Friedman test for the lid treatment showed that the proportion of opaque lids accessed was significantly different across the ten choices ($\chi^2_9$=28.549, p=0.001). Pairwise

comparisons with Bonferroni corrections showed significant differences in the following choices: 3-9, 3-10. The Friedman test for the cork treatment on the proportion of opaque corks chosen across choice numbers was not significantly different across the ten choices ($\chi^2_9$=9.136, p=0.425). The Friedman test for the membrane treatment on the proportion of opaque membrane chosen across choice numbers was significantly different across the ten choices ($\chi^2_9$=63.345, p<0.0001). Pairwise comparisons with Bonferroni corrections showed significant differences in the following choices: 1-8, 1-9, 1-10, 2-8, 2-9, 2-10, 3-10, 4-8, 4-9, 4-10. Appendix 3 shows the full statistic parameters of the pairwise comparisons.

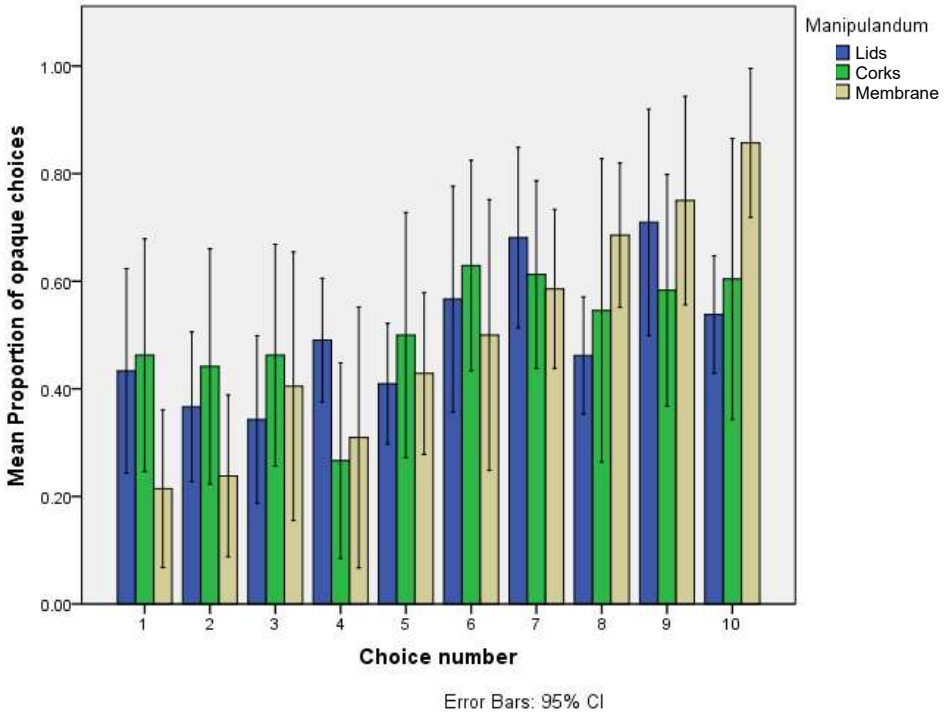



Figure 5.12 - Mean proportion of holes covered by an opaque manipulandum (versus transparent) accessed in each choice of the 10-choice sequence. See text for significant choice-numbers pairs. Means calculated across subjects and sessions.

### 5.3.5 Experiment 3 – Manipulandum preferences

A multiple regression was performed to determine if manipulandum type (i.e. the two manipulandum options on the board, one referred to as “chosen” and one as “alternative”) predicted the proportion of chosen manipulandum. If kea were presented with manipulanda A and B, choosing to work for a reward covered by A meant A was the chosen manipulandum and B the alternative. Only data from the first five choices (out of ten) were used since considering a full session would not return a preference. For example, if kea received manipulanda A and B in a session, they would choose A five times and B five

times. Analyses on the ten choices would have found no overall preference. Limiting the analysis to five trials allowed to investigate subjects' preferences based on the proportion of those five choices used for manipulandum A or B: five choices for A would indicate a preference for A. Regression analysis showed that there was independence of residuals, as assessed by a Durbin-Watson statistic of 1.427. There was homoscedasticity, as assessed by visual inspection of a plot of studentized residuals versus unstandardized predicted values. There was no evidence of multicollinearity, as assessed by tolerance values greater than 0.1. There were no studentized deleted residuals greater than ±3 standard deviations, no leverage values greater than 0.2, and values for Cook's distance above 1. The assumption of normality was met, as assessed by a Q-Q Plot. $R^2$ for the overall model was 1.6% with an adjusted $R^2$ of 1.1%, a small size effect according to Cohen (1988). Chosen manipulandum and alternative manipulandum significantly predicted the proportion of chosen manipulandum, $F_{2, 388}$=3.109, $p$=0.046. Alternative (i.e. non-chosen) manipulandum and chosen manipulandum added statistically significantly to the prediction (Table 5.6). Table 5.7 shows the mean proportion of choices for all kea for a given manipulandum against the alternative manipulandum.

Table 5.6 – Regression coefficients for the model predicting the proportion of chosen manipulandum.

| Variable | Unstandardised β | Coefficient Standard Error | Standardised β | t | p |
|---|---|---|---|---|---|
| Constant | 0.615 | 0.064 | | 9.666 | <0.001 |
| Alternative manipulandum | -0.026 | 0.013 | -0.119 | -2.042 | 0.042 |
| Chosen manipulandum | -0.058 | 0.025 | -0.132 | -2.262 | 0.024 |

Table 5.7 - Mean proportions for choosing a focal manipulandum given a specific alternative. Mean values calculated across all subjects and sessions.

| Focal manipulandum | Alternative manipulandum | Proportion of choices towards focal manipulandum |
|---|---|---|
| Opaque lids | Opaque membrane | 0.49 |
| Opaque corks | Opaque membrane | 0.42 |
| Transparent lids | Transparent membrane | 0.46 |
| Transparent corks | Transparent membrane | 0.43 |
| Transparent corks | Transparent lids | 0.43 |
| Opaque corks | Opaque lids | 0.52 |

## 5.4 Discussion

In this study, several experiments were conducted to determine whether visual and physical task-related characteristics affected a potential contrafreeloading response in captive kea. Contrafreeloading was observed as kea retrieved food rewards covered by a manipulandum while uncovered food rewards were simultaneously available.

### 5.4.1 Experiment 1A - Do kea (prefer to) contrafreeload in a foraging task by rotating transparent lids?

Kea were able to manipulate transparent lids on the foraging board in the first training session. Five birds required more than one session to learn to rotate the lids to access a pellet. From these, three were the youngest subjects. Their learning curve to rotate lids was probably due to their reduced experience in experiments involving apparatus manipulation combined with their greater interest in object-exploration and object-play (Diamond and Bond, 1999). The other two kea could have had a reduced exploration drive or, alternatively, their proficiency at rotating lids could just be an effect of individual differences (e.g. Auersperg et al., 2011). It is known that when solving a task, kea might attempt unsuccessful manipulations even after trying a successful action (e.g. Miyata et al., 2011). No kea were found to attempt other manipulations after being trained to rotate the lids.

Sessions conducted to assess performance differences when pellets were covered or uncovered showed a low number of kea manipulating lids that did not cover a pellet, suggesting that kea were able to discriminate between covered / uncovered and rewarded / non-rewarded holes but it is possible that the four subjects who interacted with futile lids were not able to perform said discriminations. Research on a starlings (*Sturnus vulgaris*) also used transparent membranes to cover food rewards and subjects were able to identify them (Bean et al., 1999), suggesting that kea should be able to see the rewards (even though avian vision shows inter-specific differences, Spetch and Weisman, 2012).

Similar experiments assessing contrafreeloading have not quantified the work or effort contrast between the free and non-free conditions (e.g. Bean et al., 1996; Forkman, 1996). To address this, manipulation time (MT) data were collected and compared between covered and uncovered sessions. MT was found to be significantly higher in the covered condition, as expected. MT data only included instances in which a bird either physically interacted with the lids or took a pellet out from the hole. This showed that kea were working more when foraging in the covered-holes version of the task.

### 5.4.2 Experiment 1B – Do kea (prefer to) contrafreeload in a foraging task with different transparent manipulanda?

Kea frequently manipulated corks outside of a pellet-retrieval situation, indicating that cork manipulation could be intrinsically reinforcing. Corks and lids were made of the same materials and both included an additional metallic element to facilitate rotation / lifting. Unlike lids, corks were not attached to the wooden board and the metallic element was not affixed to the plastic element, allowing it to rattle. These differences could make corks more attractive. Experimental protocols included a control for this possibility since corks were available during the uncovered-pellet condition (scattered on and around the board). If corks were attractive, kea would be expected to interact with them at equal levels in the covered and uncovered conditions. This was not the case: when corks covered access to all pellets, all but one kea interacted with non-functional corks (all corks were functional at the beginning of a session; once a cork was removed from a hole it became non-functional). Only three kea manipulated non-functional corks during the uncovered condition (all corks were non-functional at the beginning of a session). This difference suggested that kea distinguished conditions, potentially understanding that object manipulation was necessary only in the covered condition.

Similar numbers of kea manipulated non-functional membranes during covered and uncovered conditions. Neophilic responses could account for these interactions as this was a novel material. Some species have been shown to prefer destructible toys (*Pan troglodytes* in Brent and Stone, 1998; *Sus scrofa* in Van de Weerd et al., 2003; *Amazona amazonica* in Kim et al., 2009) which could explain membrane interactions. Once a membrane was removed from a hole, it often ripped. A preference based on destructibility would have been expected for all subjects, which was not the case as only half of the subjects interacted with membranes.

For both transparent membranes and corks, MT was found to be significantly higher when manipulanda covered food rewards than when they were uncovered. This suggested that the covered condition did involve work. In the main testing phase, kea displayed a tendency to use their first choices to retrieve free pellets and started to work for pellets once the free options were exhausted. Yet, their second choice was almost equally divided between covered and uncovered holes. This distribution would be expected in choice 5 or 6 (when no free pellets would be left). When transparent membranes covered half the number of pellets, kea showed a weaker preference (albeit non-significant) to access the covered pellets in their last choices. Their choices showed similar frequency levels between covered and uncovered choices. These data indicated a weaker freeloading tendency when

transparent membranes covered pellets and a preference for transparent membrane interaction.

### 5.4.3 Experiment 1C – Do kea (prefer to) contrafreeload in a foraging task when non-free food is occluded?

Results showed that choice order was a significant predictor of the proportion of covered holes accessed when opaque lids, membranes and corks were provided. Kea showed a preference to access uncovered holes first across the three manipulanda. Although not statistically tested, this preference appeared stronger when opaque lids or opaque membranes covered the holes. This was partially evidenced by the lower number of significant pairwise comparisons for choice order during the cork treatment. Also, first and last choices (out of ten) during the opaque cork setup included frequencies for both free and non-free pellets, when, for example, first choices during the membrane and lid treatments were mostly towards uncovered rewards. Bean and colleagues (1999) found that starlings (*S. vulgaris*) contrafreeloaded less when information about food was visually assessed. The data from this experiment contradicted these results as kea preferred to access covered holes earlier in their choices when they could not see the pellet requiring work.

### 5.4.4 Experiment 2 – Foraging preferences in terms of reward visibility

If kea were choosing which pellet to retrieve based on visibility, they should retrieve the pellets covered by the transparent manipulanda in their first choices. Figure 5.12 showed that proportions of opaque manipulandum choices during earlier choices were higher with corks, followed by lids and the lowest with membranes. This indicated that kea were more flexible in their choices when membranes covered food rewards. This pattern was similar with lids, but the preference was weaker as proportion for covered rewards was higher and pairwise comparisons only showed one significant choice pair. When rewards were covered by corks, subjects appeared to choose randomly. These results indicated that kea preferred transparent options, but this preference was not significant with corks as manipulandum.

All rewards were covered in this experiment; therefore, responses cannot be explained in terms of contrafreeloading. If a preference for transparency had affected kea's responses, then results would have been similar across all three manipulanda, but it was not the case. Therefore, some other aspect of the manipulanda might have influenced responses. The most evident difference between manipulanda related to their physical appearance. Kea have been shown to highly engage in haptic exploration (Auersperg et al., 2011) and inserting combinations (Auersperg et al., 2014). The corks allowed the most

haptic exploration as they were made of a circular piece of acrylic with a bolt and a nut, and kea were able to separate corks from the board.

### 5.4.5 Experiment 3 – Manipulandum preferences

Kea showed the following preferences: pellets covered with transparent membranes were chosen earlier than those with transparent lids; pellets covered with opaque membranes were accessed earlier than opaque lids; pellets covered with transparent membranes were accessed earlier than transparent corks; pellets covered with transparent lids were accessed earlier than transparent corks; pellets covered with opaque membranes were accessed earlier than opaque corks; and pellets covered with opaque corks were accessed earlier than opaque lids. Overall, transparent membranes appeared to be preferred as kea interacted earlier with this manipulandum when compared with corks and lids.

Two studies have assessed captive kea's preferences for objects and tasks. Auersperg and colleagues (2011) tested kea retrieving a reward by either pulling a string, opening a window, inserting a marble into a tube, or inserting and moving a stick. All subjects showed a preference to solve the task by pulling the string, with opening a window and inserting a marble as the second and third preferred manipulations. Authors explained the string-pulling preference in terms of either it being the most visually distinctive tool or chosen due to habituation, as kea had been previously exposed to string-pulling setups. Auersperg and colleagues (2014) exposed kea to a set of boards with holes, vertical tubes, vertical hollow cylinders, or horizontal hollow cylinders. Blue, red, and yellow balls, rings, cubes, and sticks of three different sizes were simultaneously available to analyse how kea combined objects with the board. Kea performed more inserting actions with tubes and preferred ball-shaped objects. These preferences were discussed by three explanations: 1) training or previous experience (also shown to affect the contrafreeloading response, Ignis et al., 1997); 2) anatomical facilitation as kea possess two pairs of opposing toes (zygodactyly; Forshaw, 2006) which are advantageous for grasping and lifting and a beak with a long mandible and pronounced curvature which complicates oral manipulations (Auersperg et al., 2011); or 3) a reinforcing effect from the stimuli. In the present study, subjects had no previous experience with similar manipulanda, thus negating the first explanation. All manipulanda were attached to the board, thus feet manipulations were not required, and kea's beaks were not found to be disadvantageous to manipulate any manipulanda, probably due to their small size, thus negating the second explanation. The third explanation appeared plausible, as corks included a piece of acrylic that could rattle (see Figure 5.4),

which could be reinforcing, but kea did not prefer these: kea showed a preference for membrane manipulation.

Wild kea are infamous for their recurrent destructive behaviour (Diamond and Bond, 1999), to the point of media often displaying kea destroying items from human visitors in their home range. Research on other parrot species has found a preference to destroy. Webb and colleagues (2010) showed that Amazon parrots (*Amazona amazonica*) preferred non-frayed over frayed rope. Two explanations were provided: one assuming oral manipulation of rope substituting preening behaviour and another one in terms of agency (see Chapter 1.3.6). Kim and colleagues (2009) found a preference in *A. amazonica* towards manipulating destructible cubes (against items of less destructible materials). They discussed this preference by citing studies on chimpanzees (*Pan troglodytes*; Videan et al., 2005) and domestic pigs (Van de Weerd et al., 2003) to show how destructible items may elicit greater manipulation activity and maintain "animal-material interactions". The pig study omitted hypotheses on why pigs would prefer "destructibility" but the chimpanzee study "predicted that destructible items—as the most controllable—would be used most frequently", which was the case. However, it did not provide a justification of why "controllable" items were preferred. The preference towards membranes in the present experiment dids not seem be a substitute behaviour (e.g. preening, Webb et al., 2010) as interactions mostly occurred to reveal a food reward. Agency did not seem to explain this preference either, as the board and manipulanda were operated but not modified.

### 5.4.6 General discussion

Kea contrafreeloaded as they foraged from covered holes while uncovered holes contained a food reward, showed a preference to retrieve uncovered pellets first and covered pellets last, showed a preference to retrieve rewards covered by transparent rather than opaque manipulanda, suggesting that kea were not exploring to obtain information about the reward, and preferred to manipulate membranes more than corks and lids, suggesting that the former may be intrinsically rewarding.

Results are partly explained by contrafreeloading explanations (see Chapter 1.3.6). While the apparatus did not include any visual or auditory cues that could reinforce subjects, manipulandum differences could be reinforcing. Lids could not be removed them from their position while corks and membranes were detachable, allowing for greater manipulation diversity. After retrieving a pellet, some kea would take it to the nearest water source to soak it before eating it. During training sessions, kea always had access to ten manipulanda: five covering holes and five spread on the ground or on the apparatus. This protocol controlled for manipulandum reinforcement, as kea would have been expected to interact with the five

manipulanda spread on the ground or apparatus, which was not the case. The overall result of transparent membranes being manipulated earlier than opaque membranes (Figure 5.12) could be alternatively explained by a reinforcing characteristic of the material. Transparent membranes, made of cellophane, could be more appealing due to light reflection. For example, corvids have been reported to show a preference to cache colourful objects (Kabicher, 1996 as cited in Bugnyar et al., 2007).

Another explanation for the membrane preference could be previous training. Kea received training sessions to ensure they were able to operate the manipulanda. Training was only conducted for the transparent manipulanda, with separate sessions for covered and uncovered rewards. Inglis et al. (1997) reviewed how training shapes the contrafreeloading response when subjects were taught to obtain food by performing an operant task and then given the choice to perform the task with free food also available. The initial training creates a habituation effect, which may carry over to choice-tests. The fact that kea were trained with transparent manipulanda could affect their preference by either choosing transparent manipulanda due to habituation or choosing opaque manipulanda due to neophilia. Experiment 2 provided evidence for the habituation effect as kea preferred transparent lids and membranes over their opaque counterparts. It may be argued that the contrast between opaque and transparent lids and corks is different from that of membranes given the material differences. It is possible that kea's perception of the task differed between type of manipulandum and these differences may explain their responses. Wild kea are known for their demolition and destructive activities (Diamond and Bond, 1999) even outside of a foraging context. Assuming these behaviours are either intrinsically or extrinsically reinforced, kea should show a greater interest in manipulating membranes, as they were the most destructible materials. Experiment 3 provided evidence for this preference, as membranes were preferred over corks and lids.

Many contrafreeloading studies require animals to forage for either free or non-free food from two separate feeders or locations (e.g. Vasconcellos et al., 2012; Van Os et al., 2017). Here, kea had to access food rewards placed in holes spaced ca. 5 cm apart on one foraging board. It could be argued that kea perceived the whole setup as one foraging opportunity and not as two conditions. Before conducting this experiment, a pilot study was conducted in which two foraging boards were provided, one containing holes with free food and the other with non-free food. A wooden shape (square or triangle) was located close to each board to act as a treatment cue. Unfortunately, kea did not learn to associate cues with a treatment type and kea displayed a side bias, choosing the board to the right during the pilot study. For this reason, the task was adapted to only use one apparatus and minimise side bias.

The most likely explanation for the obtained results refers to the nature of the task. As discussed by de Jonge et al. (2008), characteristics of operant tasks and test situations may play a role in contrafreeloading. If these are natural (i.e. promoting species-specific behaviours) they facilitate the contrafreeloading response and ensure subjects' engagement. The foraging behaviour of wild kea has been described as diverse and extensive, including behaviours such as excavating, demolishing, and scraping (Diamond and Bond, 1999). The results of this chapter have shown that kea contrafreeload and that this response was independent of type of manipulandum and visual access to the reward. It also showed that there was no significant preference to contrafreeload but there was a significant preference to manipulate membranes.

These results are valuable for the husbandry of captive kea. Chapter 2 showed that kea enrichment relied on the provision of browse, puzzle feeders, boxes, scatter feeding, and food concealed in cages. Opportunities including transparent or opaque membranes could increase enrichment diversity and promote engagement with the devices, possibly having a greater well-being impact.

### 5.5 Conclusions

- Kea were able to retrieve pellets covered by lids, corks, or membranes. This process took at least four times more work (measured as duration to retrieve pellets) than when pellets were uncovered (i.e. free).

- Kea were shown to contrafreeload in all experiments as they always retrieved at least one covered pellet while uncovered pellets were still available. However, kea showed a "freeloading" preference, as they tended to retrieve all uncovered pellets first and then retrieve covered pellets.

- Kea showed a weaker contrafreeloading response when the covering manipulanda prevented visual access to pellets.

- Comparisons between transparent and opaque manipulanda showed significant preferences to access pellets covered by transparent manipulanda first.

- Comparisons between manipulandum types showed that kea preferred to retrieve pellets covered by transparent and opaque membranes compared to pellets covered with corks or lids.

# Chapter 6. Challenge preferences: do kea show a preference for levels of difficulty in a cognitive task?

## Abstract

Challenges such as locating food resources or avoiding predators are common in the wild ecology of many wild animals. Behavioural theories based on optimisation (e.g. optimal foraging) hypothesise that animals should seek the maximum reward with the minimum effort but research on captive animals has found that this is not always the case. Farm animals interact with operant discrimination tasks to gain access to a resource even when the same resource is available without the need of solving a task. This preference has been linked with positive effects on well-being based on physiological indicators. This study was designed to investigate if kea preferred solving an easy or difficult version of a cognitive task, with a minimal physical component, to obtain a food reward. First, kea were trained to associate an image as the positive cue predicting a food reward. Then, the positive cue was presented with increasing numbers of negative distractor cues. Kea's performance (i.e. mistakes made per session) was used to select two levels of the task to function as the easy and difficult options. Kea were trained to navigate a T-maze and then free access to the T-maze was provided. One arm contained the easy task and the other the difficult task. Subjects' choices were measured throughout the experiment. A follow-up study was performed with a more difficult version of the difficult task and with the T-maze rotated 45° and 90°. Some subjects displayed a side bias, as they exclusively chose the right arm of the T-maze. The remaining subjects showed individual preferences towards task difficulty; at the group level, the difficult task was more likely to be chosen. Rotating the T-maze influenced arm choices, as biased subjects changed their response. Providing a more difficult task affected subjects' preferences, as they became less explorative of the T-maze.

## 6.1 Introduction

Wild animals frequently face different challenges to survive and thrive. For example, nesting species need to find adequate locations to build their nests (e.g. Kolbe and Janzen, 2002), males of lekking species need to defeat their competitors to attract females (Fiske et al., 1998), and extractive foragers must learn appropriate techniques to gain access to embedded foods (e.g. Diamond and Bond, 2009). Choosing to solve or ignore some of these challenges may not be an option, as ignoring them could decrease their fitness. Animal behaviour theories suggest that, given the choice, animals should avoid time and energy-consuming challenges. The optimal foraging hypothesis assumes that natural selection shaped foraging behaviour to maximise energy gain (per unit time) by optimising the cost:benefit ratio of foraging actions (Pierce and Ollason, 1987). When animals forage in an area with high resource availability, they are expected to spend most of their time in this location to maximise energy intake (assuming the food patch has a high mean and low variance of food resources and fitness being a linear function of these parameters, see Pyke, 1984; Shettleworth, 2010) and depart the foraging area if the resources are depleted or if animals are no longer acquiring information about the location (Pyke, 1984). In a general (and extreme) case, animals could be hypothesised to avoid challenges that minimise energy intake.

Contrafreeloading, which occurs when an animal obtains resources by working instead of retrieving a simultaneously available, identical resource (Inglis et al., 1996) appears to contradict this hypothesis. Chapter 1.3.6 detailed the possible explanations of why contrafreeloading occurs, which include: preference for self-assessment of abilities and for gaining information when resources are uncertain, “working” causing secondary reinforcement, or sensory reinforcement due to changes occurring when working for food (e.g. visual or auditory cues occurring during operant tasks; Inglis et al., 1997). Clark (2017) provided a brief discussion on contrafreeloading based on exploring resources by discussing how “the process of exploring and acquiring a resource seems to be more important than the resource *per se*”. She also added that exploration may be a behavioural need and that satisfying this need improves animal well-being (see Jensen and Toates, 1993 and Chapter 1 of this thesis).

Meehan and Mench (2007) discussed how providing challenges to captive animals can make them use or exercise their cognitive abilities and natural behaviours, parting from their discussion on how wild animals face and cope with challenges, resulting in positive effects on their fitness. The concept of “appropriate challenges” has been used to refer to “problems that may elicit frustration, but are potentially solvable or escapable through the application of cognitive and behavioural skills” and have been suggested to be linked with

positive effects on animal well-being (Meehan and Mench, 2007). For example, pigs (*Sus scrofa*) showed reduced aggression, more exploration and fewer fear responses when obtaining a reward by solving a cognitive task than pigs who did not receive the task (Zebunke et al., 2013). Oesterwind and colleagues (2016) showed that solving a visual discrimination task enhanced curiosity (i.e. exploration) of dwarf goats (*Capra aegagrus hircus*) compared to those not receiving the task. Chimpanzee (*Pan troglodytes*) and dolphin (*Tursiops truncatus*) play behaviour was enhanced when challenges in the form of mazes were present in their enclosures (Clark and Smith, 2013; Clark et al., 2013). Cows receiving a food reward by solving an operant task appeared more excited than cows receiving food rewards without performing any task (Hagan and Broom, 2004). Also, providing puzzle feeders to primates reduced the expression of stereotypical behaviours (Murphy, 1976; Novak et al., 1998).

Wild kea are no stranger to challenges. Their natural habitat is described as a "rigorous and unforgiving environment" (Diamond and Bond, 1999). Beech forests are an important food source for kea, but they can be an unreliable resource due to seasonality (Aspinall, 1967). Kea have evolved to be omnivorous generalists and they have thrived because of their "ability to make use of whatever resources chance brings its way" (Diamond and Bond, 1999). From an evolutionary perspective, kea were likely selected to explore and exploit challenges. Kea and kaka (*Nestor meridionalis*) diverged from a common ancestor who presumably became separated into two populations, one in the north and one in the south of New Zealand (Diamond and Bond, 1999). The southern region was characterised for its harsher and colder environments and the ancestral population in this region evolved behavioural strategies to cope with these challenging habitat became kea (Diamond and Bond, 1999).

Given their "challenging" status quo, it can be argued that kea have, if not a preference, a tolerance for challenges. A videoclip from BBC Earth (2009) showed wild kea removing wooden logs deliberately placed over rubbish bins to prevent kea from opening them, it did not take long for a kea to remove the logs. The video also showed kea being tested on problem-solving with a slanted stick holding a cylinder containing peanut butter. The only way to access peanut butter was by sliding the cylinder upwards until it came off the stick. The video probably showed the most eye-catching scene, which cannot be interpreted as a preference for solving tasks, as kea could have had several attempts or solved the task because of due to a preference for peanut butter (Schwing, pers. comm.). These observations do suggest that wild kea are not averse to tasks or challenges.

Wild kea are described as “bold, curious, and ingeniously destructive” (Huber and Gajdon, 2006) and research on captive kea shows the extent of their curiosity and neophilia. For example, kea were faster than ravens (*Corvus corax*) in finding the solutions of a problem-solving and tool-use paradigm (Auersperg et al., 2011), result attributed to kea’s haptic exploration and keenness to manipulate novel objects (Auersperg et al., 2011). Gajdon and colleagues (2011) tested if kea used social information to solve a tool-use task, finding that exposure to a conspecific solving the task improved subjects’ proficiency, but kea stopped solving the task and started exploring other (non-functional) manipulations.

Chapters 4 and 5 investigated kea’s motivation towards physical challenges in terms of contrafreeloading, finding that kea foraged by manipulating rocks, wooden blocks (Chapter 4), lids, membranes and corks (Chapter 5) blocking food when free food was also freely available. Kea were found to forage at similar levels from trays with and without rocks and wooden blocks (Chapter 4) and preferred to freeload when lids, membranes and corks covered food rewards (Chapter 5). It is possible that the physical manipulations required to forage were not perceived as a challenge or were not cognitively demanding. Considering kea as “physically dexterous” (i.e. able to engage and solve physical tasks, e.g. Diamond and Bond, 1999) either by anatomical (e.g. curved beak) or behavioural (exploration and neophilia) adaptations, the physical aspect of tasks or challenges could be less relevant than their cognitive component. But how is this “cognitive component” defined?

Clark (2017) recognised that defining and measuring this cognitive component is not easy to be (visually) identified but did not provide an explicit definition of this concept. Instead, she described cases of positive reinforcement training “when it is unlikely that animals would learn how to perform these tasks” as examples of tasks with a cognitive component. Following her rationale, providing captive kea with novel tasks may be a way to exercise their cognitive capacities. If these tasks have varying difficulties, kea may display preferences that align with earlier predictions: kea prefer *difficult cognitive* challenges. Recent research suggests this might be the case.

Farm-based studies on cognitive enrichment focus on providing operant tasks to get a reward (see Chapter 1.6.2). For example, Langbein and colleagues (2009) gave goats (*C. hircus*) the choice of obtaining water from one of two devices. Both devices had a button that dispensed water, but one required solving a visual discrimination task to become functional. Analysis on the number of button presses and water consumed at each device showed that, while goats obtained most of their water from the dispenser lacking the discrimination task, they also engaged with the dispenser including the discrimination task (which partly agrees with the results of Chapter 4 where kea spent more time at free food trays but also

frequented trays with objects, but Langbein and colleagues' protocol does not qualify as contrafreeloading as there was no free water concurrently available). Ernst and colleagues (2005) trained pigs (*S. scrofa*) to discriminate an individually assigned acoustic cue to obtain a food reward. Pigs then had to press a button with an increasing fixed ratio upon hearing their acoustic cue to obtain food. Pigs were shown to engage with these challenges over 12 h daily with success rates of up to 95%. Follow-up experiments showed that providing farm animals with these "cognitive challenges" has positive effects on their well-being in terms of physiology and behaviour (Langbein et al., 2004; Puppe et al., 2007; Zebunke et al., 2013; see Chapter 1.4.2).

There is a separate body of literature where animals are given two identical tasks to obtain a reward with one task being more *difficult* than the other to determine subjects' preferences. These studies belong to the framework of traditional learning theories, predicting that animals should prefer to work with less effort and shorter reinforcement delays (e.g. Hull, 1943; Skinner, 1938) rather than the well-being framework.

For example, Clement et al. (2000) trained pigeons to colour-discriminate visual cues as positive (food reward delivered) or negative (no reward). Two groups were trained with the following protocols: one received a negative cue and a positive cue, both requiring one peck to deliver food (low work); the other received a negative cue and a positive cue (different from the first group) requiring 20 pecks to deliver food (high work). Pigeons then received either the two positive cues or the two negative cues to determine how they responded. Data showed that pigeons pecked more the positive cue requiring 20 pecks than at the positive cue requiring one peck and pecked more the negative cue requiring 20 pecks than the negative cue requiring one peck. In other words, pigeons preferred the stimuli associated with more work. Friedrich and Zental (2004) presented pigeons with two identical feeders and first determined baseline preferences for either. Later, pigeons were trained to peck 30 times to forage from their less-preferred feeder or one time to forage from their more-preferred feeder. Data showed that subjects had a significant increase in preference for the originally non-preferred feeder (i.e. the feeder associated with more pecks). Kacelnik and Marsh (2002) trained starlings (*Sturnus vulgaris*) to fly across their cages either 4 or 16 times before receiving one of two visual reinforcers followed by a food reward. When starlings were given the choice to access both reinforcers without flying, they showed a preference towards the reinforcer associated with flying 16 times. Johnson and Gallagher (2011) trained mice (*M. musculus*) to press one lever to receive glucose or another lever to receive Polycose®. When given the choice to operate both levers, mice showed a preference for glucose. After training subjects to press 15 times to receive Polycose®, mice's preferences shifted and now preferred Polycose®.

The examples above are not fully explained by contrafreeloading theories as there was never free food concurrently available. Instead, animals had the choice of performing the same task but with varying difficulties. The research on cognitive enrichment and difficulty preferences seems to indicate that captive animals are capable of successfully interacting with complex physical and cognitive tasks and these may even have a positive effect on their well-being (Langbein et al., 2004; Puppe et al., 2007; Zebunke et al., 2013) but studies do not distinguish cognitive from physical challenges. As defined by Shettleworth (2001), (animal) cognition refers to "perception, learning, memory, and decision making […] in which animals take the information about the world through senses, process, retain and decide to act on it". The experiments described as cognitive enrichment still relied on the physical component of the "acting on" process (e.g. pushing buttons or pressing levers).

The objective of this chapter is to provide a cognitive challenge with a minimal physical component. For this, an experimental design was needed where tactile interactions were minimised. Visual discrimination tasks are common in the fields of animal behaviour and cognition (e.g.: insects: Perry and Barron, 2013; fish: Kuba el al., 2010; poultry: Kuhne et al., 2011; wild birds: Templeton and Gonzalez, 2004; rodents: Trevino, 2014; reptiles: Davis and Burghardt, 2012; mammals: Byosiere et al., 2017). Carducci and colleagues (2018) compared kea and capuchin monkeys (*Sapajus* spp.) on their performance in a visual discrimination task with and without access to tactile information, finding that both species showed comparable levels of accuracy in solving the task. Wein and colleagues (2015) analysed visual recognition when stimuli were pictures or real objects, concluding that pictures were suitable stimuli for cognitive tests based on kea's discrimination proficiency. The present experiment relies on solving a visual discrimination task as the cognitive component, which aligns with Langbein and colleagues' (2009) concept of cognitive enrichment. The overarching aim of this study is to provide kea with a visual discrimination task of varying difficulty to determine if kea showed a preference for more or less difficulty, expecting a preference for difficult challenges given their ecology and their exploratory drive.

## 6.2 Methods

The experiment was performed in the Kea Lab, Austria between October and December 2016 and between August and September 2017 (see Chapter 5.2.1 for further information). This experiment was divided into the following stages.

Stage 1 – Finding Wally training: kea learned that discriminating the option displaying the positive visual stimulus resulted in obtaining a food reward.

Stage 2 – Level difficulty assessment: visual stimuli were arranged in different ways (i.e. levels) to determine kea's performance.

Stage 3 – T-maze training: kea were trained to navigate a T-maze.

Stage 4 – Preference tests: kea were presented the actual preference test, in which one easy and one difficult task were provided.

Stage 5 – Preference tests follow-ups: preference tests were modified in three ways: the T-maze arm containing the easy and difficult tasks were reversed; the difficult task was replaced with a more difficult level; the T-maze was rotated.

### 6.2.1 Subjects

Eleven kea from the group at the Haidlhof Research Station took part in this study (Table 6.1; see Chapter 5.2.2 for details on husbandry and management). Sessions took place in one set of two compartments in visual isolation from conspecifics (Figure 6.1).

Table 6.1 – List of kea that participated in this experiment. Further information on their husbandry in Chapter 5.2.2.

| Kea | Age (years) | Sex |
|---|---|---|
| Anu | 9 | Male |
| Jean-Luc | 1 | Male |
| John | 17 | Male |
| Kermit | 12 | Male |
| Lilly | 9 | Female |
| Papu | 3 | Female |
| Pick | 12 | Male |
| Plume | 9 | Female |
| Roku | 8 | Male |
| Sunny | 9 | Female |
| Willy | 9 | Female |

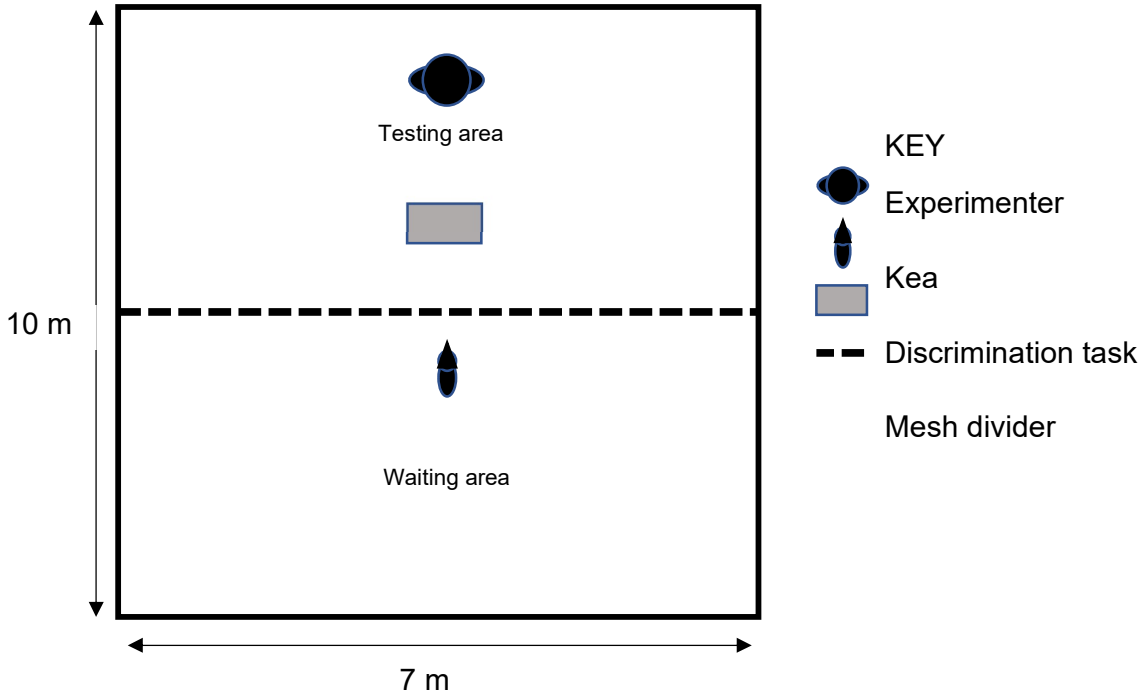



Figure 6.1 – Schematics of the experimental compartment. The testing area was Porticula Res and the waiting area Porticula Expectatio (see Figure 5.1).

### 6.2.2 General protocols and visual cues

During experimental sessions (hereafter, a session implies a set of 20 sequential trials unless stated otherwise), kea were either called by their name or asked to hop on the experimenter's arm and taken into the compartment. Once inside, kea waited in "waiting area" while the experimenter prepared the setup in the testing area. Setting up consisted in placing two wooden stands at an equal distance from the entry point and inserting a positive cue in one stand and a negative cue in the other (Figure 6.2). A food reward (one Nutribird pellet) was placed behind the positive cue; nothing was placed behind the negative cue.

A trial started when the experimenter opened the mesh divider between the waiting and testing areas. Afterwards, a kea walked towards one of the two stands and inspected behind it. Kea had been previously exposed to a similar setup as part of a quantity discrimination experiment (unpublished data) so they had experience in finding rewards behind boards like these. If a kea explored behind the positive (i.e. rewarded) board, they could retrieve the pellet, walk back to the waiting compartment, and eat it. If the kea explored behind the negative cue (i.e. non-rewarded), the researcher ushered the kea back to the waiting compartment and closed the divider. The researcher then arranged new cues. The location of the positive and negative cues was randomised across trials and sessions by a coin toss, controlling that the positive cue was not presented on the same side for more than

three consecutive trials (this prevented the development of positional bias; see Gellermann, 1933). Testing stopped if a kea refused to enter the testing compartment in two consecutive trials.

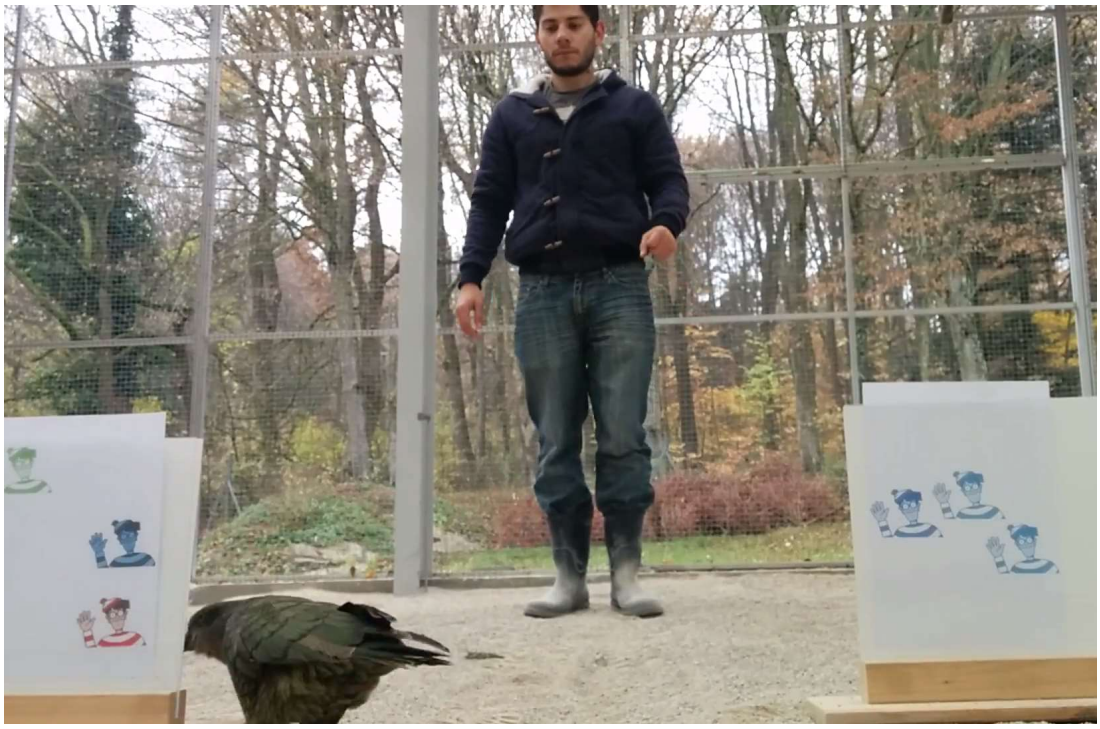


Figure 6.2 – A kea successfully solving a discrimination task during Stage 2. The researcher was aware of the possibility of a "Clever Hans" effect (see Sebeok and Rosenthal, 1981) and adapted the protocol to control for this possibility: the testing area was blocked by an opaque divider, the researcher opened the divider remotely by a rope, standing still and looking at a fixed point in the horizon every trial.

Looking in the literature for information to design visual stimuli did not provide clear results as experiments often use images without providing any rationale. For example, Geller et al. (2004) and Schmitt (2019) only mention ***how*** rats and primates were shown specific images such as clipart, geometrical forms, or photographs but not ***why***. Rationale for visual stimuli is almost exclusive to studies utilising them to demonstrate a cognitive concept (e.g. "abstraction levels" by differentiating between two images pertaining, or not, to a category in Vonk and MacDonald, 2002; 2004; and Vonk et al., 2012). Another criterion to choose visual stimuli is animals' visual capacity. Research on pigeons has shown that they can discriminate between: images with and without humans, images with animals and objects, and between images from Monet and Picasso's art (Castro and Wasserman, 2014). Research on five parrot species (including kea) and four non-psittacine birds (O-Hara et al.,

2017) relating to visual discrimination presented subjects images with straight or curved edges of varying colours and shapes (Figure 6.3, left). O-Hara and colleagues did not provide a rationale for choosing these stimuli. Wein and colleagues (2015) discussed the lack of research on how non-human animals perceive visual stimuli and performed a visual discrimination experiment to investigate kea's perception. Their stimuli included 2D images on a screen and actual photographs, both representing a real object (see Figure 6.3, right). Their results were not conclusive in terms of kea being able to form an internal representation of 3D objects but brought "support to the use of pictures in cognitive research with this species". Laboratory research on parrot vision with budgerigars (*Melopsittacus undulatus*) as a model species has shown that budgerigars' colour photoreceptors absorb light peaks in the red, green, blue and ultraviolet sections of the spectrum (Berg and Bennet, 2010) with research on grey parrots (*Psittacus erithacus*) showing comparable conclusions (Ödeen and Håstad, 2003). There are no studies exploring the vision system of the kea. However, information is available via a study on bait colour that showed kea found yellow, brown, and red food items more often than blue and green items (Weser and Ross, 2013). The same preference was found when assessing food item retrieval and consumption (Weser and Ross, 2013). Following from O'Hara' et al. (2017) and the research on other parrots on colour perception, predefined shapes from Microsoft Word and an image of the "Where's Wally?" character were used to create as visual stimuli (Figure 6.4). Since the aim of this study is not to prove kea's interpretation of the images, the relevance of visual stimuli was not paramount. "Wally" was chosen as it included colours like those of other shapes and enabled witty wordplay when presenting this research. Furthermore, Wein et al. (2017) supported the use of any type of 2D images. Positive cues always included the figure of Wally, negative cues never did. Shapes were arranged depending on the level (Tables 6.2 and 6.3) and printed on A4 paper.

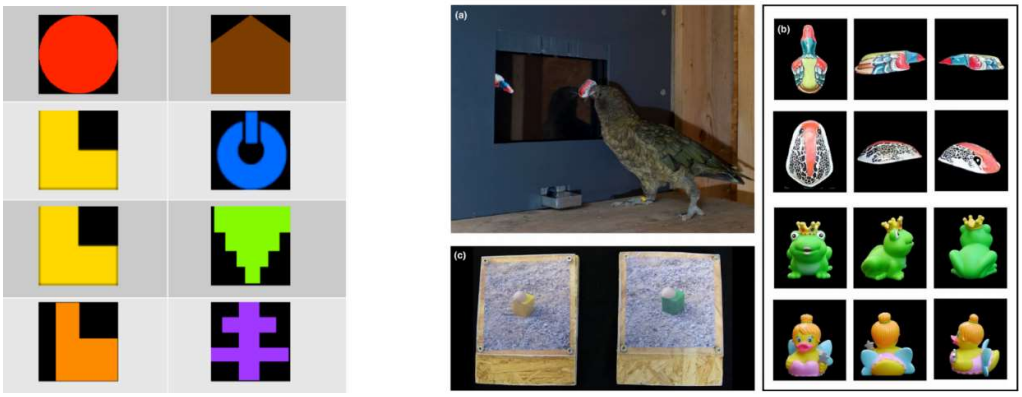



Figure 6.3 – Some examples of visual stimuli utilised in visual discrimination tests on captive kea. Left: O-Hara et al., 2017; Right: Wein et al., 2015.

Figure 6.4 - Shapes used during testing (shown at 30% zoom level). Shapes were arranged in several configurations to create the different levels (see Tables 6.2 and 6.3).

### 6.2.3 Stage 1: Finding Wally training

Kea were trained to associate the Wally image as a positive cue. Four levels were implemented (Table 6.2). In Level T4, white panels were placed between the waiting and testing areas (Figure 6.5) to visually block the setup process and to ensure subjects solved the task only after they gained access to the test area and not beforehand, as they could see the visual cues in the time it took the experimenter to open the divider. Kea were considered trained once they completed all four levels according to criteria[17]: finding Wally (i.e. choosing the positive cue) with 100% accuracy in one session or 85% accuracy or better in two consecutive sessions.

[17] Criteria were suggested by Schwing, R., head of the Kea Lab.

Figure 6.5 - Testing setup. Sliding mesh (shown in the open position) was closed whilst setting up the visual task then opened for a kea to enter and perform the task.

Table 6.2 – Training levels and examples of corresponding visual cues. Column “Example (+)” shows an example of a positive cue; column “Example (-)” shows an example of a negative cue.

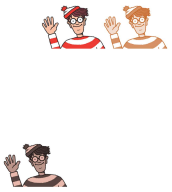
| Level | Description | Example (+) | Example (-) |
|---|---|---|---|
| T1 | Wally always on the centre of the positive cue with no other figures. No figures on the negative cue. |  | |
| T2 | Wally on different positions on the positive cue with no other figures. No figures on the negative cue. |  | |
| T3 | Positive cue as in Level T2. One shape on the negative cue (different shapes and locations of shape). |  |  |
| T4 | Same cues as in Level T3 but including a visual barrier to avoid incidental cueing from the setup process. | | |

### 6.2.4 Stage 2: Level difficulty assessment

Six levels were designed in which the type, number, location, and colour of the visual cues varied (Table 6.3). Testing protocols and success criteria were as in Stage 1. The purpose of this assessment was to quantify levels’ difficulty. For every trial, the experimenter took note of each subjects’ choice (left or right, and positive or negative cues). The number

of choices for the negative cue per session were totalled and used to measure each level's difficulty.

Table 6.3 – Levels for difficulty analysis in Stage 2. Column "Example (+)" shows an example of a positive cue; column "Example (-)" shows an example of a negative cue. Over 100 cues were used.

| Level | Description | Example (+) | Example (-) |
|---|---|---|---|
| E1 | Same cues as in Level T3. |  |  |
| E2 | Three shapes. Twenty positive and twenty negative cues varying in shapes and location of shapes. |  |  |
| E3 | Eight shapes. Twenty positive and twenty negative cues varying shapes and location of shapes. |  |  |
| E4 | Three Wally figures. Twenty positive and twenty negative cues varying in colour and location of Wally figures. |  |  |
| E5 | Nine shapes. Twenty positive and twenty negative cues varying in colour and location of Wally figures. |  |  |
| E6 | Nine shapes. Nine positive cues varying in location of Wally. Only one negative cue (there was no variation in the shapes or colours). |  |  |

### 6.2.5 Stage 3: T-maze training

A T-maze was designed to present two visual discrimination tasks simultaneously (Figure 6.4). In this setup, kea faced two tasks: 1) choosing the left or right path of the T-maze and 2) solving the corresponding discrimination task. The decision corridor (see Figure 6.4) was necessary to occlude the visual discrimination tasks prior to choosing a path because kea should first decide which path to follow and then solve the corresponding task. One side of the T-maze always contained an easy task and the other side a difficult task (assessed by performance in Stage 2). The sides of the T-maze with the easy and difficult task were counterbalanced across subjects.

This was the first-time kea were tested in a T-maze. To habituate subjects with the T-maze, two sessions of forced exploration (FE) were conducted. FE consisted in blocking one of the two T-maze arms so that kea were forced to go to the unblocked option. FE was needed to make sure kea had experience in accessing both T-maze chambers. Each arm of the T-maze was blocked for 5 consecutive trials. After these, the unblocked side became blocked for the next 5 trials and so on until 20 trials were completed. The initial T-maze arm blocked was counterbalanced across subjects. During FE sessions, the researcher took note if the kea solved the visual discrimination task successfully or not.

Testing protocols were as in previous stages. First, the experimenter would set the discrimination tasks while a kea was in the waiting compartment. Next, the mesh divider was opened, the kea entered the decision corridor and walked left or right. Once a kea accessed a T-maze arm, it solved the discrimination task. If a subject solved the discrimination task correctly, they collected the food reward and returned to the waiting compartment to eat it. If a kea did not solve the discrimination task correctly, the researcher ushered the kea back to the waiting area.

### 6.2.6 Stage 4: Preference tests

After T-maze training, kea received up to eight sessions of free exploration (E) with both arms unblocked. During E sessions, the experimenter took note of the subjects' chosen arm and if they solved the discrimination task successfully or not. These sessions constituted the preference test.

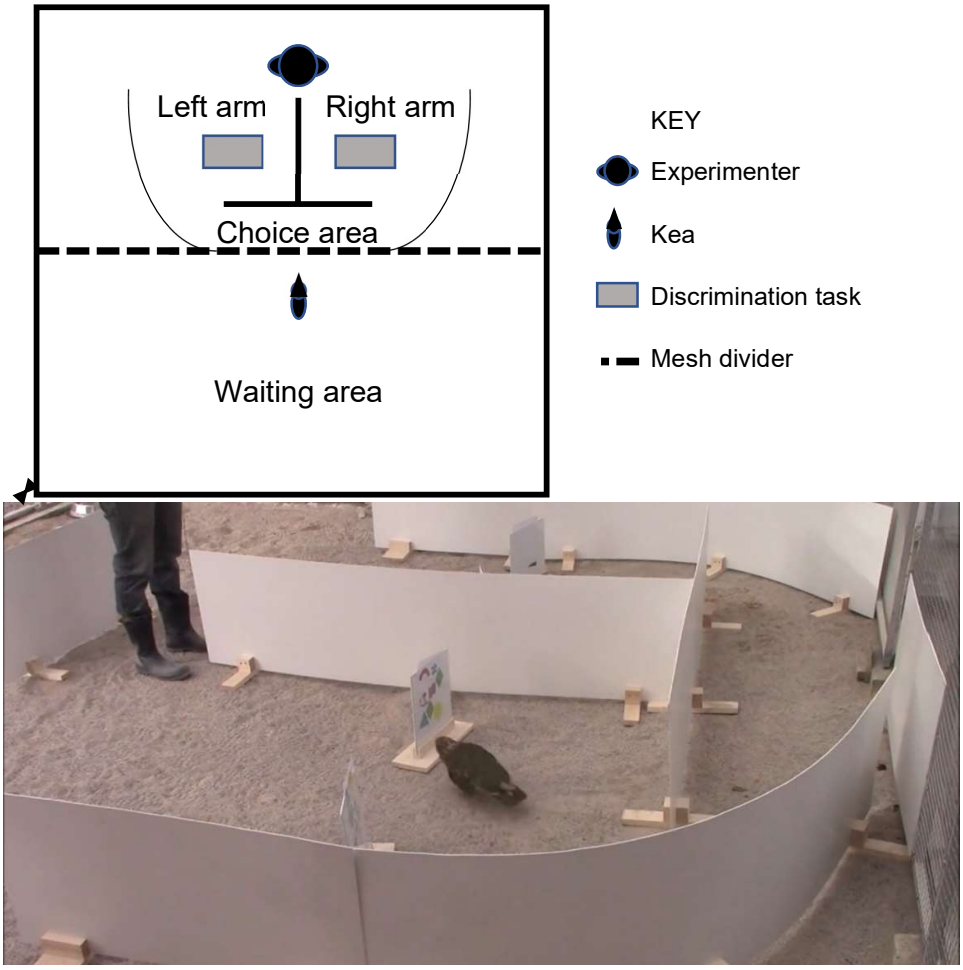



Figure 6.6 – T-maze from Stages 4 and 5. Top: Compartment schematics. Bottom: A kea choosing the left arm and successfully solving the discrimination task.

### 6.2.7 Stage 5: Preference tests (follow-up)

A second round of E tests was performed eight months later to determine if (1) preferences were maintained and if (2) the orientation of the T-maze or (3) a more difficult difficult task influenced kea's choices. Before formal testing occurred, all subjects received one session of forced exploration to reacquaint them with the apparatus and the discrimination task.

#### 6.2.7.1 Stage 5.1: Reversal

Kea received up to seven sessions with protocols as per Stage 4 but with the T-maze arms and task difficulties reversed (i.e. kea having the difficult task in the right arm in Stage 4 now had the easy task in the right arm).

#### 6.2.7.2 Stage 5.2: More difficult task

Kea received up to three sessions in which the difficult task was replaced with a more difficult level (Level E5). Subjects that displayed a lateralized response (more than 85% of choices for the same side) during Stage 5.1 had a T-maze arm – task difficulty reversal (i.e. kea having the difficult task in the right arm in Stage 5.1 now had the easy task in the right arm).

#### 6.2.7.3 Stage 5.3: T-maze orientation

To determine if the T-maze's position in respect to the testing compartment influenced subjects' arm choice, the T-maze was rotated 90° and 45° (Figure 6.7). Kea received up to two sessions with the T-maze rotated 90° and up to four sessions with the T-maze rotated 45°. Table 6.4 shows the characteristics of all sessions across Stages 4-5.3.

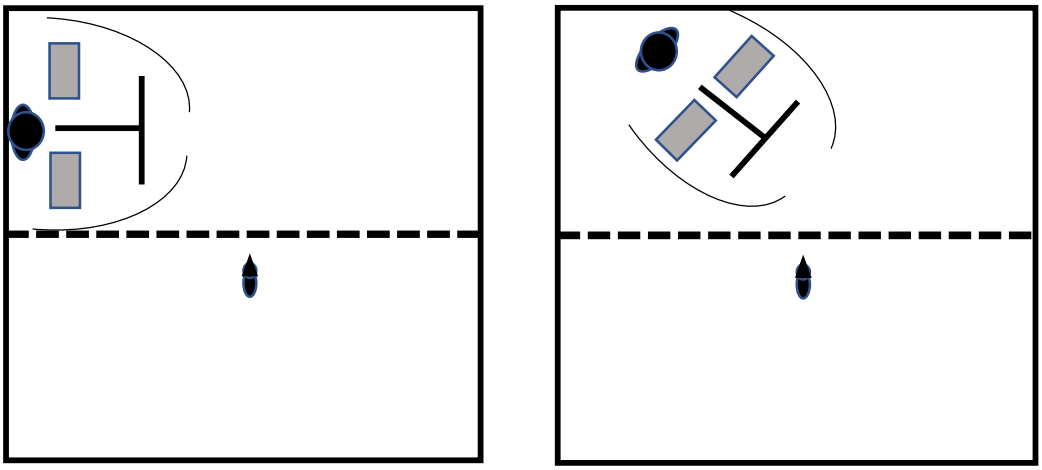


Figure 6.7 – Setup for Stage 5.3. Left: diagram of the arena after a 90° rotation. Right: diagram of the arena after a 45° rotation.

#### 6.2.7.4 Overall analysis

Data from Stages 4, 5.1, 5.2, and 5.3 were pooled and used to determine overall preferences. Binomial tests were performed with data for proportion of chosen difficult tasks to determine if they deviated from a random preference (i.e. choosing a task 50% of choices). Two binomial logistic regressions were performed using Subject, Session, Trial, Location of Difficult Task, T-maze Orientation, Type of Difficult Task and Year of Testing as variables predicting Chosen Difficulty to determine which of these factors correlated with subjects' choices and with Exploration Index.

Table 6.4 – Session details for Stages 4, 5, 5.1, 5.2 and 5.3. DR = difficult task in the right T-maze arm. ER = easy task in the right T-maze arm. Shaded cells = follow-up sessions (Stage 5). 90° = T-maze rotated 90° degrees counterclockwise. 45° = T-maze rotated 45° counterclockwise. Red text = difficult task replaced with a more difficult level (see Section 6.2.6). Differences in the number of sessions across subjects and stages due to subjects showing a biased response or a lack of interest in participating in testing (see text for further details).

| | | Kea | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Stage** | **Session** | **Anu** | **Jean-Luc** | **John** | **Kermit** | **Lilly** | **Papu** | **Pick** | **Plume** | **Roku** | **Sunny** | **Willy** |
| 4 | 1 | DR | ER | DR | ER | ER | DR | ER | DR | ER | ER | ER |
| | 2 | DR | ER | DR | ER | ER | ER | ER | DR | ER | ER | DR |
| | 3 | DR | ER | DR | ER | ER | DR | ER | DR | ER | ER | DR |
| | 4 | ER | ER | DR | DR | ER | DR | DR | DR | DR | ER | DR |
| | 5 | | ER | DR | | ER | | | | | ER | DR |
| | 6 | | ER | DR | | ER | | | | | ER | DR |
| | 7 | | ER | DR | | ER | | | | | ER | DR |
| | 8 | | ER | DR | | ER | | | | | ER | DR |
| 5.1 | 1 | ER | DR | ER | DR | DR | ER | DR | ER | DR | DR | ER |
| | 2 | ER | DR | ER | DR | DR | ER | DR | ER | DR | DR | ER |
| | 3 | ER | DR | ER | DR | DR | ER | DR | ER | DR | DR | ER |
| | 4 | ER | DR | ER | | DR | ER | | ER | | DR | ER |
| | 5 | ER | DR | ER | | DR | ER | | ER | | DR | |
| | 6 | | DR | ER | | DR | | | ER | | | |
| | 7 | | DR | ER | | DR | | | ER | | | |
| 5.2 | 1 | DR | DR | ER | DR | DR | DR | DR | DR | DR | DR | ER |
| | 2 | DR | DR | DR | DR | ER | DR | DR | DR | DR | ER | ER |
| | 3 | | ER | DR | | ER | DR | | DR | | DR | ER |
| | 4 | | | | | | | | | | ER | DR |
| 5.3 | 1 | DR / 90° | ER / 90° | DR / 90° | ER / 90° | ER / 90° | DR / 90° | ER / 90° | DR / 90° | ER / 90° | ER / 90° | DR / 90° |
| | 2 | ER / 90° | DR / 90° | ER / 90° | DR / 90° | ER / 90° | ER / 90° | DR / 90° | ER / 90° | DR / 90° | DR / 90° | ER / 45° |
| | 3 | DR / 45° | ER / 45° | ER / 45° | ER / 45° | ER / 45° | DR / 45° | ER / 45° | DR / 45° | ER / 45° | ER / 45° | DR / 45° |
| | 4 | DR / 45° | DR / 45° | ER / 45° | DR / 45° | DR / 45° | ER / 45° | DR / 45° | DR / 45° | DR / 45° | DR / 45° | DR / 45° |
| | 5 | | DR / 45° | DR / 45° | ER / 45° | ER / 45° | DR / 45° | ER / 45° | DR / 45° | ER / 45° | | |
| | 6 | | ER /45° | DR / 45° | ER / 45° | | DR / 45° | | | | | |

### 6.2.8 Behaviour coding and analysis

Two variables were computed with the data from Stages 1 and 2. “Sessions to reach criteria” (S2C) was calculated by adding the number of sessions needed to complete a level according to criteria. “Success rate” (SR) was calculated with the proportion of choices for the positive cue during a session. Friedman tests were performed on these variables to determine significant differences across levels. If necessary, pairwise comparisons between all levels were performed.

Two variables were calculated with the preference test data from Stages 4, 5.1, 5.2 and 5.3. Chosen difficulty (CD) was calculated as the proportion of trials per session in which the difficult task was chosen. Exploration index (EI) was calculated as the number of times a kea chose an arm different from their previous choice during a session. For example, a kea choosing the same T-maze arm during a session would have an EI of zero; a kea alternating T-maze arm every trial would have an EI of 19. Binomial tests were performed to compare CD to a hypothetical value of 0.5 (the assumed value if kea were choosing with no preference). All binomial tests include an observed sample of 20 (trials) except where indicated. Two binomial logistic regressions were performed with dichotomous data for CD and EI as predicted outcome and Subject, Session, Trial (only for chosen task), Location of the difficult task (left or right arm), T-maze orientation (0°, 45° or 90°), Hard task modality (hard task from Stage 4 or harder task from Stage 5.2) and Year of testing (2016 or 2017) as predictor variables with data from each subjects’ sessions in Stages 4, 5.1, 5.2, and 5.3. Statistical tests were performed on SPSS 24 (IBM©). Significance was determined according to $\alpha=0.05$ unless otherwise stated. Two-tailed statistics were used to determine significance in binomial tests. Since binomial tests involved multiple comparisons, the Benjamini-Hochberg-Yekutieli procedure was used to correct the significance level. This procedure was chosen as it is less conservative than other methods and it deals with dependent comparisons (Benjamini and Yekutieli, 2001).

## 6.3 Stage 1: Finding Wally training

### 6.3.1 Results

Training comprised a total of 77 sessions. Level T1 required more sessions to reach criteria than Levels T2, T3 and T4, each of which a median of just one session. Figure 6.8 shows the median number of sessions kea required to reach criteria for each level. All kea completed the training regime except for one subject, who, due to a mistake from the researcher, skipped Level T2. S2C was significantly different across levels, $\chi^2(3) = 23.35$, $p<0.0005$. Pairwise comparisons were performed with a Bonferroni correction for multiple

comparisons. Statistical significance was accepted at the $p<0.0125$ level. S2C was statistically significantly different between Levels T1-T2, T1-T3 and T1-T4 (Table 6.5).

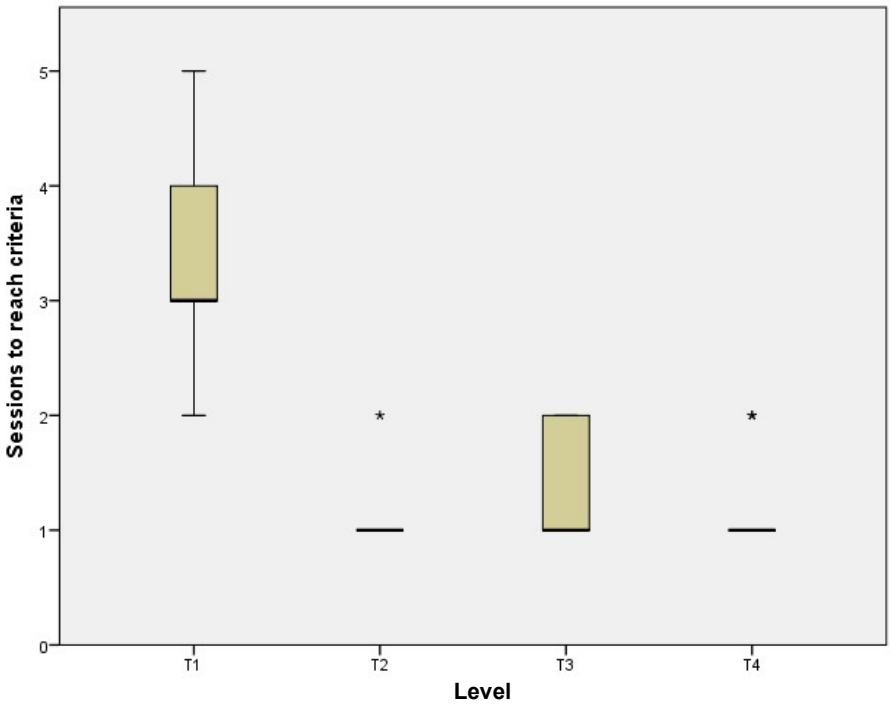



Figure 6.8 – Boxplot for median number of sessions until reaching criteria (100% accuracy in one session or 85% accuracy or better in two consecutive sessions) in training sessions. *Two outliers were found in Level T2 and two in Level T4.

Table 6.5 – Pairwise comparisons of sessions to reach criteria across training levels. **indicates significance according to p<0.0125 (corrected for multiple comparisons).

| Comparison | Test statistic | Standard Error | p |
|---|---|---|---|
| T1-T2 | 2.00 | 0.550 | 0.001** |
| T1-T3 | 1.77 | 0.550 | 0.001** |
| T1-T4 | 0.273 | 0.550 | 0.620 |
| T2-T3 | -0.227 | 0.550 | 0.680 |
| T2-T4 | 0.045 | 0.550 | 0.934 |
| T3-T4 | 0.273 | 0.550 | 0.620 |

### 6.3.2 Discussion

Kea required the most sessions to reach criteria for Level T1 (discriminating a board with one image versus a board with no image). This result is not surprising as this was their first exposure to the task and stimuli. For the three remaining levels, where a non-rewarded image was added to one board and the position of images on the boards varied (Levels T2,

T3 and T4), no kea required more than two sessions to reach criteria. These results suggest that after Level T1, kea had learned to associate the positive cue (Wally figure) as the positive stimulus.

## 6.4 Stage 2: Level difficulty assessment

### 6.4.1 Results

Figure 6.9 shows the median number of sessions needed to reach criteria across levels. S2C was statistically different across levels (Friedman's ANOVA; $\chi^2(5) = 22.516$, $p<0.005$). Pairwise comparisons were performed with a Bonferroni correction for multiple comparisons, showing significant differences between Levels E1 and E3 (Table 6.6). Level E1 posed the least difficulty as all kea but two managed to reach criterion in the first session. Level E2 saw an increased difficulty as fewer kea succeeded in the first session and two kea required four sessions. No kea was able to reach criteria in the first session of Level E3. Level E4 saw a decrease in difficulty as all but four subjects succeeded in the first session. Only two kea were able to complete Level E5 in one session. One kea was not able to reach criteria for Level E5 (and thus was not tested on Level E6). No kea reached criteria in Level E6. One kea required eight sessions to complete Level E3 and there was enough time to only test him once on Level E6.

Figure 6.10 shows the median SR for all subjects in each session. SR was significantly different across levels ($\chi^2(5)=37.143$, $p<0.005$). Pairwise comparisons were performed with a Bonferroni correction at the $p<0.01$ level. SR was significantly different between Levels E1-E6 ($p<0.0001$), E2-E6 ($p<0.0001$) and E4-E6 ($p<0.0001$) (Table 5.7). Median SR was the highest in Level E1. All but 2 kea had a SR of 100% in this phase. For Level E2, only five kea had a SR of 100%. No kea scored 100% in Level E3. Proficiency increased in Level E4, shown by 7 kea achieving a SR of 100% and the other 5 kea achieving a SR greater than or equal to 90%. Accuracy in choosing the positive cue fell in Level E5. Only 2 kea had a SR of 100% and the remaining subjects ranged from 77.5% to 92.5%. Level E6 had the lowest scores with the highest SR being 70% and the lowest being 40%.

Level E1 was chosen as the easy task based on its low S2C and high SR. Level E3 was chosen as the difficult task as it had a significantly higher S2C than Level E1. Furthermore, Level E3 was chosen to leave Levels E5 and E6 as available options to increase the difficulty contrast in future tests.

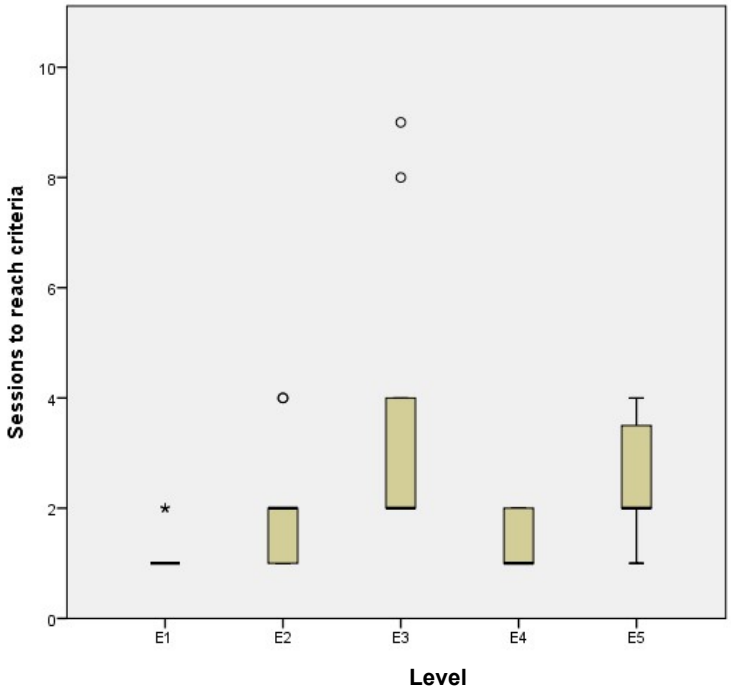



Figure 6.9 – Boxplot for median number of sessions until reaching criteria in Stage 2 for level difficulty sessions (N=11). One outlier was found in Level E1, two extreme outliers in Level E2 and two in Level E3. No kea reached criteria in Level E6.

Table 6.6 – Pairwise comparisons of sessions to criteria data across levels (except for Level E6 as no kea reached criteria). Standard error for all comparisons = 0.837.

| Comparison | Test statistic | p |
|---|---|---|
| E1-E2 | -0.950 | 1.000 |
| E1-E3 | -2.750 | 0.015 |
| E1-E4 | -0.500 | 1.00 |
| E1-E5 | -2.400 | 0.062 |
| E2-E3 | -1.800 | 0.472 |
| E2-E4 | 0.450 | 1.000 |
| E2-E5 | -1.450 | 1.000 |
| E3-E4 | 2.250 | 0.107 |
| E3-E5 | 0.350 | 1.000 |
| E4-E5 | -1.900 | 0.347 |

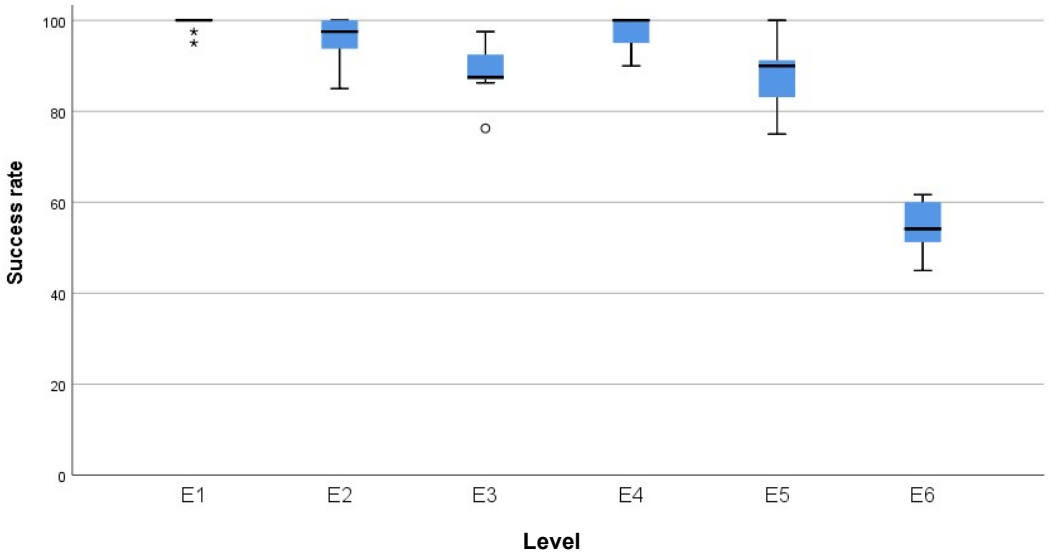



Figure 6.10 – Boxplot for median success rates (i.e. proportion of trials within a session in which kea chose the rewarded cue). Two outliers were found in Level E1 and one extreme outlier in Level E4. One kea was not tested on Level E6 due to not reaching criteria in Level E5. No kea reached criterion in Level E6 (testing stopped due to time constraints). See text above for statistical differences across sessions.

Table 6.7 – Pairwise comparisons of success rate data across. Standard Error for all comparisons = 0.837.

| Comparison | Test statistic | p |
|---|---|---|
| E1-E2 | 0.800 | 0.339 |
| E1-E3 | 2.400 | 0.062 |
| E1-E4 | 0.600 | 0.437 |
| E1-E5 | 2.450 | 0.051 |
| E1-E6 | 4.250 | <0.001 |
| E2-E3 | 1.600 | 0.837 |
| E2-E4 | -0.200 | 1.000 |
| E2-E5 | 1.650 | 0.729 |
| E2-E6 | 3.450 | 0.001 |
| E3-E4 | -1.800 | 0.472 |
| E3-E5 | 0.050 | 1.000 |
| E3-E6 | 1.850 | 0.405 |
| E4-E5 | 1.850 | 0.405 |
| E4-E6 | 3.650 | <0.001 |
| E5-E6 | 1.800 | 0.472 |

### 6.4.2 Discussion

Six levels were created by increasing the number of non-rewarded images on positive and negative cues and changing their position and colour. Kea were tested with these stimuli to determine the number of Sessions to Reach Criteria (S2C) and evaluate each level's difficulty. Looking at the median S2C of Levels E1 – E5, the order of difficulty was as follows (from least difficult to most difficult): E1, E4, E2, E5, E3. Level E6 was assumed to be the most difficult level since no kea reached criterion (however some kea were not tested on this level). Only Levels E1 (one figure per cue), E2 (three figures per cue), E3 (eight figures per cue) and E6 (nine identical figures of similar colour per cue) conformed to their predicted difficulty, as they ranked increasing S2C apart from E6, where criterion was never reached. Difficulty did not increase in Level E4 (three figures of the same type but different colour) as shown by the decrease in S2C in most kea. This study does not allow to conclude on the exact method by which kea solved the task. It is possible that kea had learned to search for specific characteristics of the Wally figure such as red stripes, skin colour, hair colour, or a combination of these.

For Level E5, the same shapes as in Level E4 were used, but now nine figures were displayed instead of three. Level E5 saw an increase in difficulty when compared to Level E4, as expected. Unexpectedly, Level E5 was less difficult than Level E3. Seven kea required more sessions to complete Level E3 than to complete Level E5. To successfully complete Level 3, kea had to discriminate the board with the positive cue among additional cues differing in shape and colour. In Level E5, kea had to discriminate only based on colour, as all boards contained the same shape in varying colours (Wally image). It may be assumed that kea struggled to discriminate the positive cue when the background images differed in shape and colour (Level E3) than when the background images differed only in colour (Level E5). This assumption is in agreement with previous research on pigeons where subjects performed better in a visual discrimination task identifying a positive cue based on one feature (colour or shape) than in a test where both features were combined (Cook, 1992). The struggle to discriminate based on shape and colour was further evidence by higher S2C and lower SR in Level E2 than Level E4. The present methods did not allow to investigate the exact mechanism by which kea solved the task; further research with an appropriate methodology (e.g. tasks controlling for shape and colour) is recommended. Level E6 had the lowest SR and no kea was able to reach criteria. The six images used in this level were of identical shape as the positive stimulus, but all had a red colouration (the positive stimulus never changed throughout Stages). Data from this level supported the theory of kea focusing on the red stripes of the unedited Wally to solve the task as all shapes had a red colouration, making Wally less conspicuous than on Levels E4 and E5.

Continuous testing on the discrimination tasks could confound the results due to intra and inter-session learning. Frequent exposure to visual tasks has resulted in performance improvements (Ahissar and Hochstein, 1997). Intra-problem learning occurs when performance changes due to successive trials (Miles, 1965). For example, pigeons receiving reversal discrimination tasks showed continuous improvement across successive reversals (Ploog and Williams, 2010). Data from Stage 2 showed that this learning effect did not impact all levels, as the mean number of correct choices in the first session of each level did not increase across levels (values were 19.8, 19.2, 17.8, 19.2, 17.5 and 9.6).

## 6.5 Stage 3: T-maze training

### 6.5.1 Results

Kea were able to navigate the T-maze by walking from the waiting compartment to the choice area and then to the unblocked arm. All kea completed both sessions of Forced Exploration. Figure 6.11 shows SR data for each discrimination task in both sessions. Both tasks had a median SR of 100. Eight kea solved the easy task perfectly in the first session and all kea in the second session. Six kea solved the difficult task perfectly in the first session and nine in the second session. The easy task (Level E1) had a SR between 90 and 100% in the first FE session and 100% during the second FE session. The difficult task (Level E3) had a SR between 80 and 100%.

### 6.5.2 Discussion

During FE sessions, the number of errors (SR) for both tasks (E1 and E3) indicated that tasks kept their previously measured low and high difficulties. Eight kea solved the easy task (E1) perfectly in the first session and all kea solved it perfectly during the second session. The three kea with SR<100 in the first session only made one mistake. Six kea solved the difficult task (E3) perfectly in the first session and nine solved it perfectly in the second session. The five kea with SR<100 in both sessions made either one or two mistakes. Five kea solved every trial correctly in both sessions. All the remaining birds showed an improvement in their performance between the two sessions of FE. Subjects' performance on Level E3 was higher than during level difficulty assessment. This increased proficiency is most likely a consequence of a learning process across sessions. It is important to note that in FE sessions, kea received only 10 trials of each level (instead of 20 like in Stages 1 and 2).

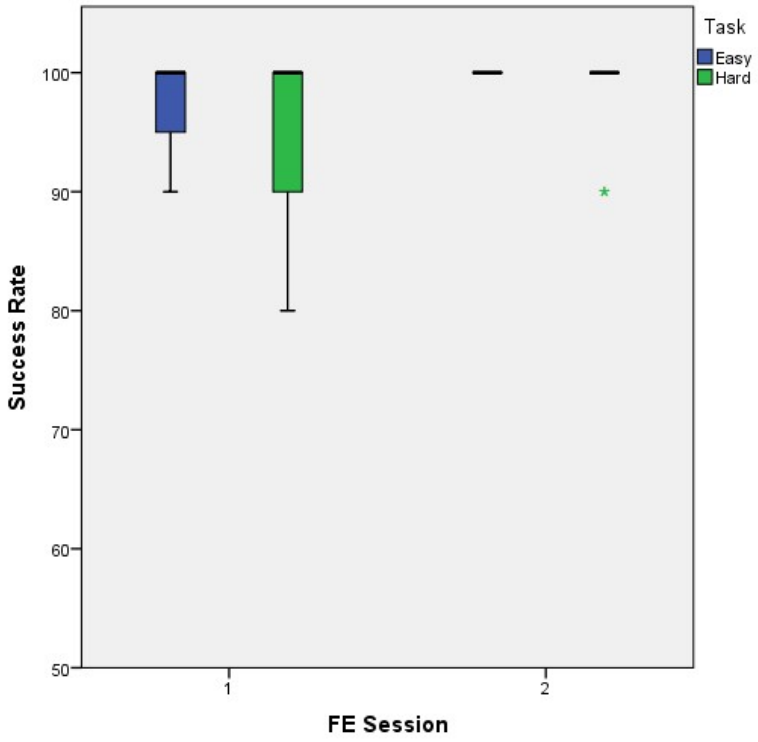



Figure 6.11 – Boxplot for Success Rates during the two forced exploration sessions. Each kea received ten easy tasks and ten difficult tasks per session. *Two outliers were found in session's 2 data for the difficult task.

## 6.6 Stage 4: Preference tests

### 6.6.1 Results

Table 6.8 presents the results from binomial tests comparing the proportion of choices for the difficult task for all subjects against a proportion of 50% (random sampling). Six subjects displayed a highly lateralised response during the first three sessions, choosing the right arm of the T-maze in 18 or more trials in at least two out of three sessions (three kea had the difficult task in the right arm and three had the easy task in the right arm). During their fourth session, the easy and difficult tasks' allocated sides were interchanged (i.e. if a kea had the difficult task on the right arm, during the fourth session the difficult task would be moved to the left arm) to corroborate if responses were side or task preferences. In this fourth session, these six kea still showed a preference for the right arm (now of 100%). These six kea were not tested further. The other five kea received four additional sessions. Figure 6.12 shows the median EI for each kea, for the group and only for the five subjects that were tested for eight sessions (dark blue line).

Table 6.8 – Binomial test results for proportion of choices for the difficult task compared to an expected proportion of 0.50. **indicates significance according to p<0.003 (corrected level).

| Kea | Session | Observed proportion | p |
|---|---|---|---|
| Anu | 1 | 0.95 | <0.001** |
| | 2 | 1 | <0.001** |
| | 3 | 1 | <0.001** |
| | 4 | 0 | <0.001** |
| Jean-Luc | 1 | 0.95 | <0.001** |
| | 2 | 0.5 | 1 |
| | 3 | 0.6 | 0.503 |
| | 4 | 0.65 | 0.263 |
| | 5 | 0.65 | 0.263 |
| | 6 | 0.65 | 0.263 |
| | 7 | 0.3 | 0.115 |
| | 8 | 0.45 | 0.824 |
| John | 1 | 0.95 | <0.001** |
| | 2 | 1 | <0.001** |
| | 3 | 0.75 | 0.041 |
| | 4 | 0.6 | 0.503 |
| | 5 | 0.5 | 1 |
| | 6 | 0.5 | 1 |
| | 7 | 0.55 | 0.824 |
| | 8 | 0.55 | 0.824 |
| Kermit | 1 | 0 | <0.001** |
| | 2 | 0 | <0.001** |
| | 3 | 0 | <0.001** |
| | 4 | 1 | <0.001** |
| Lilly | 1 | 0.2 | 0.012 |
| | 2 | 0.35 | 0.263 |
| | 3 | 0.35 | 0.263 |
| | 4 | 0.15 | 0.003 |
| | 5 | 0.15 | 0.003 |
| | 6 | 0.15 | 0.003 |
| | 7 | 0.15 | 0.003 |
| | 8 | 0.25 | 0.041 |
| Papu | 1 | 1 | <0.001** |
| | 2 | 0.1 | <0.001** |
| | 3 | 1 | <0.001** |
| | 4 | 1 | <0.001** |
| Pick | 1 | 0 | <0.001** |
| | 2 | 0 | <0.001** |

| | | | |
|---|---|---|---|
| | 3 | 0 | <0.001** |
| | 4 | 1 | <0.001** |
| Plume | 1 | 1 | <0.001** |
| | 2 | 1 | <0.001** |
| | 3 | 1 | <0.001** |
| | 4 | 1 | <0.001** |
| Roku | 1 | 0.05 | <0.001** |
| | 2 | 0 | <0.001** |
| | 3 | 0 | <0.001** |
| | 4 | 1 | <0.001** |
| Sunny | 1 | 0.25 | 0.041 |
| | 2 | 0.2 | 0.012 |
| | 3 | 0.45 | 0.824 |
| | 4 | 0.2 | 0.012 |
| | 5 | 0.3 | 0.115 |
| | 6 | 0.3 | 0.115 |
| | 7 | 0.35 | 0.263 |
| | 8 | 0.1 | <0.001** |
| Willy | 1 | 0.15 | 0.003 |
| | 2 | 0.85 | 0.003 |
| | 3 | 0.75 | 0.041 |
| | 4 | 0.7 | 0.115 |
| | 5 | 0.7 | 0.115 |
| | 6 | 0.8 | 0.012 |
| | 7 | 0.6 | 0.503 |
| | 8 | 0.75 | 0.041 |
| Group (non-lateralised kea) | 1 | 0.5 | 1.000 |
| | 2 | 0.58 | 0.133 |
| | 3 | 0.58 | 0.133 |
| | 4 | 0.46 | 0.484 |
| | 5 | 0.46 | 0.484 |
| | 6 | 0.48 | 0.764 |
| | 7 | 0.39 | 0.035 |
| | 8 | 0.42 | 0.133 |

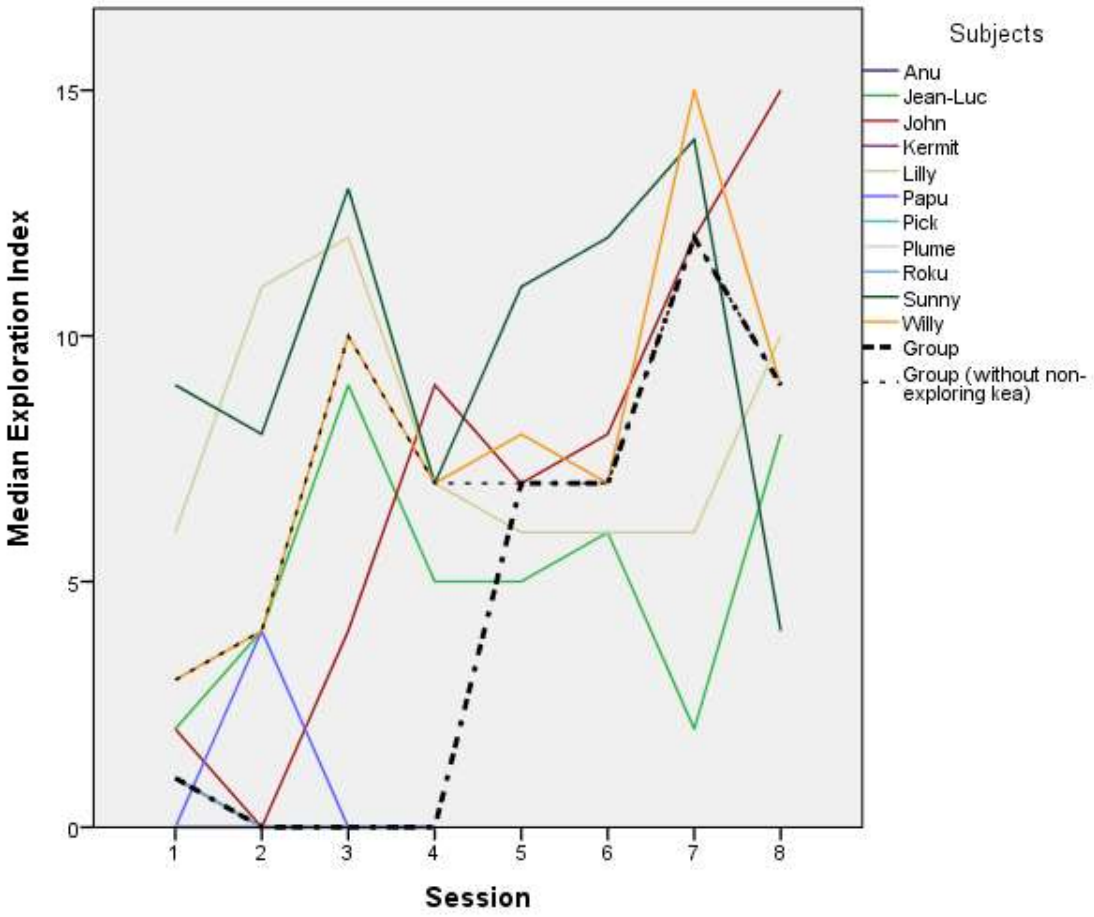



Figure 6.12 – Median Exploration Index across sessions in Stage 4. Four kea only received four sessions due to low arm-alternation behaviour.

### 6.6.2 Discussion

Data for six kea showed that they were not choosing a T-maze arm based on the task but due to a side bias (right-side preference). Innate lateralised behaviour could explain this preference. Rogers (1989) discussed how several bird species showed cognitive function laterality (e.g. singing being controlled by the left hemisphere in some species of songbirds). Eleven out of sixteen species of Australian parrots showed significant relationships between eye and foot (left) preferences when exploring objects and food items (Brown and Magat, 2011). Bhagavatula and colleagues (2014) tested budgerigars (*M. undulatus*) flying through different sets of apertures and found individual preferences to fly through a left or right path but no group preference. No study has assessed any type of lateralisation on kea. It is possible that kea possess a lateral response to navigational tasks, but this still needs to be tested.

Another explanation for lateralized responses could be the subjects' captive environment. The location of the T-maze in the experimental compartment meant that one side of the T-maze was closer to the sliding wall dividing the main enclosure (where all kea were) with the testing compartment. Auditory contact was always possible during tests, so a subject could be motivated to navigate to the side closest to its conspecifics or main living quarters: the right side). Sociality is an important aspect of kea behaviour (e.g. complex social play behaviour, Diamond and Bond, 1999). In the wild, juvenile kea remain in family groups or flocks (Jackson, 1960). In experiments with captive kea, social context has been shown to affect cooperative behaviour (Tebbich et al., 1996) and vocal production (Wein et al., 2017). It is possible that kea perceived social or environmental cues at the time of testing that influenced their chosen T-maze arm.

From the kea with no strong lateral preferences, two showed a significant preference towards one task. One kea chose the difficult task significantly more in two sessions. He also chose the difficult task (non-significantly) more in four sessions and showed no preference for either task in two sessions. Another kea chose the easy task significantly more in one session. All her other sessions showed this same preference but without significance. A third kea chose more difficult tasks in five sessions, the easy task in two and did not prefer either in one. A fourth kea always chose the easy task more. The fifth kea chose the difficult task more in all but one session, in which she preferred the easy task. The latter three kea appeared to choose either task randomly.

Exploration Index was calculated as a proxy variable for task preference. Kea with low EI were less motivated to change their previous choice and explore the alternative side; kea with high EI were motivated to seek a different choice in their next trial. Looking at the EI of the non-lateralised kea showed an increase across sessions. This could be interpreted as an increased motivation to explore a different side. In other words, at the beginning of preference testing, kea had a strong motivation to adhere to their chosen task. Towards the end of testing, kea's task preference became weaker. Comparing EI and CD data in early sessions at the group level, kea began the experiment (Session 1) with no preference for either task and low EI. For the next two sessions, kea preferred (non-significantly) the difficult task and EI increased. For the last five sessions, kea's preference shifted towards the easy task and EI continued to increase. In other words, kea seemed to develop a preference for the easy task across sessions, but they were still flexible in their choice.

The literature on animal cognition includes several reports on how subjects choose arms in T-maze experiments. Spontaneous alternation behaviour occurs when subjects change their preferred arm in a T-maze without differential reinforcement (Richman et al.,

1987). Rodents showed a “natural tendency […] to alternate their choice of goal arm (Dember and Richman, 1989). Fowls and pigeons, on the other hand, did not alternate their entry choice (Hughes, 1989). Richman et al. (1987) discussed how in the wild spontaneous alternation is displayed by a species if their foraging or exploration behaviours benefit from such alternation. The exploration and extractive foraging behaviours of kea make them candidates for spontaneous alternation. Under this premise, kea would have demonstrated high values of EI throughout testing, but this was only observed in later sessions.

It is possible that the observed choices for non-lateralized kea were confounded by experimental protocols since they always received the difficult task on the same side in all sessions. Another Stage was conducted to determine if subjects’ choices remained the same when task / T-maze arms were reversed.

## 6.7 Stage 5.1: Reversal

### 6.7.1 Results

From the six kea that preferred the right T-maze arm in Stage 4, two still chose significantly more the right T-maze arm. Another kea still chose significantly more the right arm in three out of five sessions. The last three kea did not show their previous side bias. One of them, Plume, showed a significant preference for a task in three sessions, with two directed to the difficult task and one toward the easy task. John preferred the difficult task in all but one session. Table 6.9 shows the results for binomial tests performed on CD data eight months after Stage 4. Figure 6.13 shows the median EI across sessions.

Table 6.9 – Binomial test results for proportion of choices for the difficult task during follow-up sessions. **indicates significance according to p<0.003 (corrected level).

| Kea | Session | Observed proportion (sample, if different from 20) | Expected proportion | p |
|---|---|---|---|---|
| Anu | 1 | 0.45 | 0.50 | 0.824 |
| | 2 | 0.30 | 0.50 | 0.115 |
| | 3 | 0.60 | 0.50 | 0.503 |
| | 4 | 0.00 | 0.50 | <0.001** |
| | 5 | 0.05 | 0.50 | <0.001** |
| Jean-Luc | 1 | 0.95 | 0.50 | <0.001** |
| | 2 | 0.30 | 0.50 | 0.115 |
| | 3 | 0.55 | 0.50 | 0.824 |
| | 4 | 0.60 | 0.50 | 0.503 |
| | 5 | 0.65 | 0.50 | 0.263 |
| | 6 | 0.80 | 0.50 | 0.012 |
| | 7 | 0.15 | 0.50 | 0.003 |

| | | | | |
|---|---|---|---|---|
| John | 1 | 0.50 | 0.50 | 1.000 |
| | 2 | 0.60 | 0.50 | 0.503 |
| | 3 | 0.35 | 0.50 | 0.263 |
| | 4 | 0.60 | 0.50 | 0.503 |
| | 5 | 0.70 | 0.50 | 0.115 |
| | 6 | 0.93 (15) | 0.50 | 0.001** |
| | 7 | 0.85 | 0.50 | 0.003 |
| Kermit | 1 | 0.80 | 0.50 | 0.012 |
| | 2 | 1.00 | 0.50 | <0.001** |
| | 3 | 1.00 | 0.50 | <0.001** |
| Lilly | 1 | 0.60 | 0.50 | 0.503 |
| | 2 | 0.85 | 0.50 | 0.003 |
| | 3 | 0.60 | 0.50 | 0.503 |
| | 4 | 0.50 | 0.50 | 1.000 |
| | 5 | 0.60 | 0.50 | 0.503 |
| | 6 | 0.60 | 0.50 | 0.503 |
| | 7 | 0.55 | 0.50 | 0.824 |
| Papu | 1 | 0.80 (15) | 0.50 | 0.035 |
| | 2 | 0.83 (18) | 0.50 | 0.008 |
| | 3 | 0.72 (18) | 0.50 | 0.096 |
| | 4 | 0.95 | 0.50 | <0.001** |
| | 5 | 0.95 | 0.50 | <0.001** |
| Pick | 1 | 0.70 | 0.50 | 0.115 |
| | 2 | 0.80 | 0.50 | 0.012 |
| | 3 | 0.95 | 0.50 | <0.001** |
| Plume | 1 | 0.80 | 0.50 | 0.012 |
| | 2 | 0.94 (18) | 0.50 | <0.001** |
| | 3 | 0.10 | 0.50 | <0.001** |
| | 4 | 0.00 | 0.50 | <0.001** |
| | 5 | 0.55 | 0.50 | 0.824 |
| | 6 | 0.70 | 0.50 | 0.115 |
| | 7 | 0.65 | 0.50 | 0.263 |
| Roku | 1 | 1.00 | 0.50 | <0.001** |
| | 2 | 0.90 | 0.50 | <0.001** |
| | 3 | 1.00 | 0.50 | <0.001** |
| Sunny | 1 | 0.60 | 0.50 | 0.503 |
| | 2 | 0.45 | 0.50 | 0.824 |
| | 3 | 0.67 | 0.50 | 1.000 |
| | 4 | 0.85 | 0.50 | 0.003** |
| | 5 | 0.70 | 0.50 | 0.115 |
| Willy | 1 | 0.20 | 0.50 | 0.012 |
| | 2 | 0.20 | 0.50 | 0.012 |
| | 3 | 0.33 | 0.50 | 1.000 |
| | 4 | 0.00 | 0.50 | <0.001** |
| Group (non-lateralised kea) | 1 | 0.62 | 0.50 | 0.002** |
| | 2 | 0.51 | 0.50 | 0.867 |
| | 3 | 0.55 | 0.50 | 0.279 |
| | 4 | 0.44 | 0.50 | 0.133 |
| | 5 | 0.60 | 0.50 | 0.022 |
| | 6 | 0.75 | 0.50 | <0.001** |
| | 7 | 0.55 | 0.50 | 0.434 |

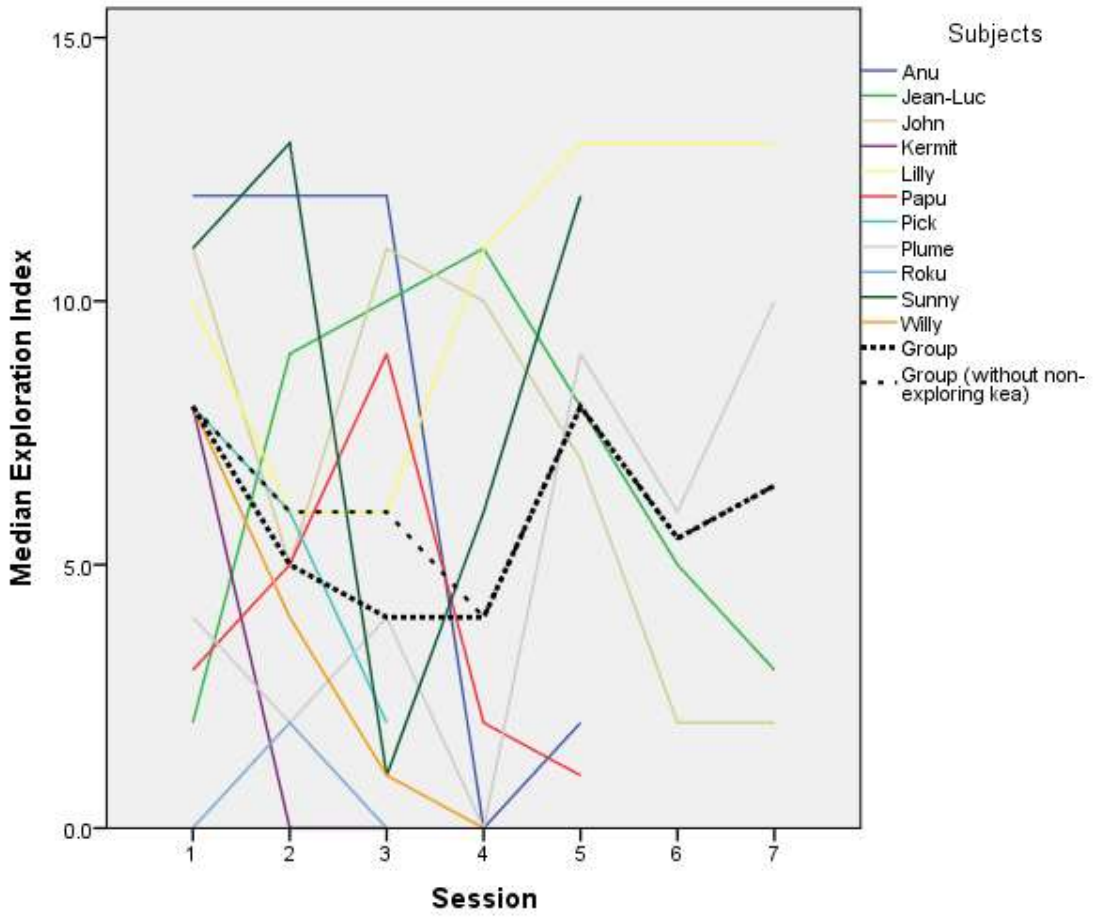



Figure 6.13 – Median Exploration Index across sessions in Stage 5.1. The Group (without non-exploring kea) line does not include data on the two kea that showed low arm-alternation behaviour.

### 6.7.2 Discussion

Comparing choices in Stage 4 and 5.1 at the group level without including data from lateralised subjects, kea chose the difficult task more in all but one session (reaching significance in sessions 1 and 6).

EI values appeared constant across sessions, which suggested that subjects were less motivated to explore an alternative T-maze arm compared to Stage 4. By the end of this Stage, kea would have received a minimum of seven and a maximum of fifteen preference sessions (between Stages 4 and 5.1). As mentioned earlier, kea could have increased their proficiency at solving either tasks with every session and, therefore, the original assessed difficulty of the difficult task would have decreased. Throughout experimental sessions, data on task resolution were still being collected. During Stage 4, subjects were solving the easy and difficult tasks with similar proficiencies (in the last four sessions only one mistake was

made when solving the difficult task). In Stage 5.1, the difficulty of the difficult task appeared to be re-established, as subjects' proficiency decreased (e.g. fifteen mistakes were made when solving the difficult task and two with the easy task). This difficulty contrast lasted for three sessions. By the fourth session, the difficulty of the difficult task decreased (e.g. just two errors across subjects).

The most evident explanation of why subjects' performance was temporarily lower in Stage 5.1 is the time separation with Stages 4 (see Table 6.4). During the eight months between Stage 4 and 5.1, some kea could have forgotten the solution to the discrimination task. Looking at other experiments, captive kea were tested on lock-opening by Miyata et al. (2011) and two of their experimental levels were five months apart. First, kea received a board with three locks and after five months kea received a board with two locks that could be in more locations. Data showed that kea had a lower performance in the later level without it increasing in later trials. Comparisons between the present work and Miyata et al. (2011) are not straightforward: in the present study kea received the exact same visual discrimination task at the two time points while Miyata et al. (2011) provided a modified physical task in the subsequent level. Another explanation for the temporary low performance at the beginning of Stage 5.1 is the reliance on exploration that kea show while solving tasks (e.g. Auersperg et al., 2011; Gajdon et al., 2011). Following this premise, kea's exploratory behaviour could have influenced their performance and subjects had to re-learn the task.

## 6.8 Stage 5.2: More difficult task

### 6.8.1 Results

Previously lateralised kea (Anu, Kermit, Pick, Roku) still showed a significant preference for the right arm. Two kea showed strong preferences for the more difficult task (even when tasks and T-maze arms were reversed). The remaining kea had different preferences in different sessions, sometimes preferring the easy task and sometimes the more difficult task. At the group level, the more difficult task was significantly preferred in two sessions and no preference for either task was shown in two sessions. EI was lower in Stage 5.2, indicating a weak interest in exploring alternative T-maze arms. Table 6.10 shows the results for binomial tests assessing preference for the difficult task during replicate sessions with the difficult task replaced with a more difficult level (Level E3 was replaced with Level E5). Figure 6.14 shows the median EI for each kea and for the group.

Table 6.10 – Binomial test results for proportion of choices for the difficult task during follow-up sessions with a more difficult difficult task. **indicates significance according to p<0.003 (corrected level).

| Kea | Session | Observed proportion (sample, if different than 20) | Expected proportion | p |
|---|---|---|---|---|
| Anu | 1 | 1.00 | 0.50 | <0.001** |
| | 2 | 0.95 | 0.50 | <0.001** |
| Jean-Luc | 1 | 0.75 | 0.50 | 0.041 |
| | 2 | 0.85 | 0.50 | 0.003 |
| | 3 | 0.30 | 0.50 | 0.115 |
| John | 1 | 0.85 | 0.50 | 0.003 |
| | 2 | 0.75 | 0.50 | 0.041 |
| | 3 | 0.30 | 0.50 | 0.115 |
| Kermit | 1 | 1.00 | 0.50 | <0.001** |
| | 2 | 0.95 | 0.50 | <0.001** |
| Lilly | 1 | 0.65 | 0.50 | 0.263 |
| | 2 | 0.35 | 0.50 | 0.263 |
| | 3 | 0.25 | 0.50 | 0.041 |
| Papu | 1 | 0.90 | 0.50 | <0.001** |
| | 2 | 1.00 | 0.50 | <0.001** |
| | 3 | 1.00 | 0.50 | <0.001** |
| Pick | 1 | 1.00 | 0.50 | <0.001** |
| | 2 | 0.95 | 0.50 | <0.001** |
| Plume | 1 | 0.90 | 0.50 | <0.001** |
| | 2 | 0.95 | 0.50 | <0.001** |
| | 3 | 0.75 | 0.50 | 0.041 |
| Roku | 1 | 1.00 | 0.50 | <0.001** |
| | 2 | 0.95 | 0.50 | <0.001** |
| Sunny | 1 | 0.75 | 0.50 | 0.041 |
| | 2 | 0.20 | 0.50 | 0.012 |
| | 3 | 0.85 | 0.50 | 0.003 |
| | 4 | 0.00 | 0.50 | <0.001** |
| Willy | 1 | 0.25 (12) | 0.50 | 0.146 |
| | 2 | 0.05 | 0.50 | <0.001** |
| | 3 | 0.05 | 0.50 | <0.001** |
| | 4 | 1.00 | 0.50 | <0.001** |
| Group | 1 | 0.83 | 0.50 | <0.001** |
| | 2 | 0.70 | 0.50 | <0.001** |
| | 3 | 0.5 | 0.50 | 1.000 |
| | 4 | 0.5 | 0.50 | 1.000 |

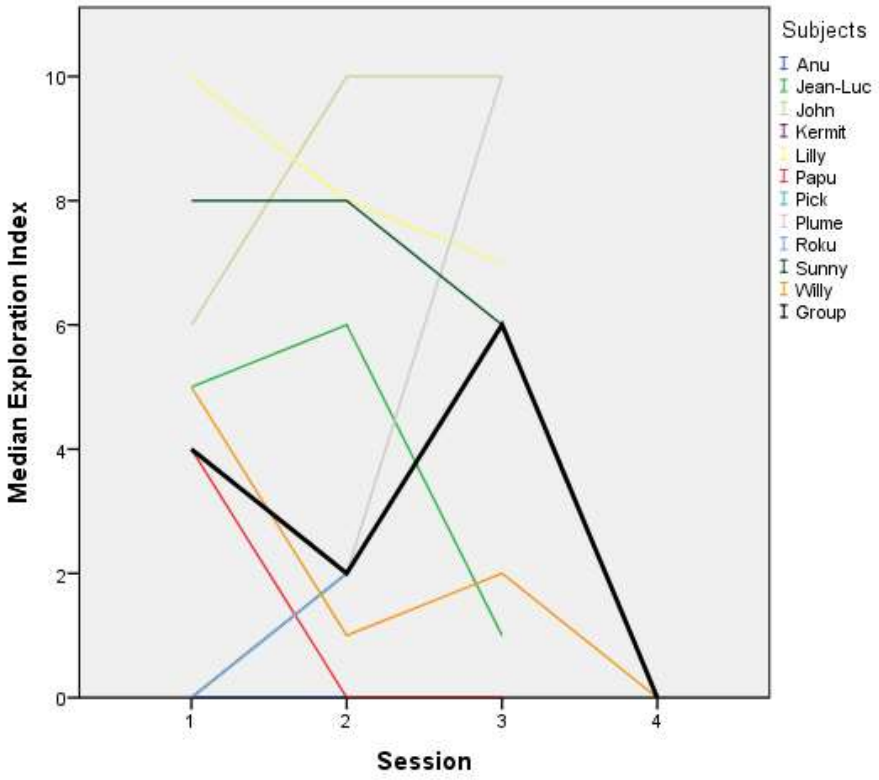



Figure 6.14 – Median Exploration Index across sessions. Kermit, Pick and Roku data overlap.

### 6.8.2 Discussion

In Stage 5.2, the difficult task was replaced with a more difficult level to increase the difficulty contrast between T-maze arms and determine if subjects' preferences from previous sessions were maintained. This difference was maintained, as overall SR was lower with the new, more difficult discrimination task compared to the previous difficult task. Comparing EI with those of Stages 4 and 5.1, EI in had a sharper decline in Stage 5.2, suggesting that kea were either being less explorative or showing a stronger preference. Looking at the data for the proportion of choices towards the difficult task (Table 6.10), overall, kea appeared to prefer the more difficult task during the first two sessions of Stage 5.2 but no preference towards either task in the last two sessions.

## 6.9 Stage 5.3: T-maze orientation

### 6.9.1 Results

Table 6.11 shows the results for binomial tests assessing preference for the difficult task during replicate sessions with the difficult task replaced with a more difficult level and the T-maze rotated 90° or 45°. Figure 6.15 shows the median EI for each kea and for the group.

Table 6.11 – Binomial test results for proportion of choices for the difficult task during follow-up sessions with a more difficult difficult task and the T-maze rotated 90° or 45°. **indicates significance according to p<0.003 (corrected level).

| Kea | Session (T-maze rotation) | Observed proportion (sample, if different than 20) | Expected Proportion | p |
|---|---|---|---|---|
| Anu | 1 (90°) | 0.10 | 0.50 | <0.001** |
| | 2 (90°) | 1.00 | 0.50 | <0.001** |
| | 3 (45°) | 0.80 | 0.50 | 0.012 |
| | 4 (45°) | 0.95 | 0.50 | <0.001** |
| Jean-Luc | 1 (90°) | 1.00 | 0.50 | <0.001** |
| | 2 (90°) | 0.00 | 0.50 | <0.001** |
| | 3 (45°) | 0.95 | 0.50 | <0.001** |
| | 4 (45°) | 0.55 | 0.50 | 0.824 |
| | 5 (45°) | 0.00 | 0.50 | <0.001** |
| | 6 (45°) | 0.95 | 0.50 | <0.001** |
| John | 1 (90°) | 0.00 | 0.50 | <0.001** |
| | 2 (90°) | 1.00 | 0.50 | <0.001** |
| | 3 (45°) | 0.14 | 0.50 | 0.001** |
| | 4 (45°) | 0.90 | 0.50 | <0.001** |
| | 5 (45°) | 0.00 | 0.50 | <0.001** |
| | 6 (45°) | 0.00 | 0.50 | <0.001** |
| Kermit | 1 (90°) | 1.00 | 0.50 | <0.001** |
| | 2 (90°) | 0.00 | 0.50 | <0.001** |
| | 3 (45°) | 0.57 | 0.50 | 0.664 |
| | 4 (45°) | 0.40 | 0.50 | 0.503 |
| | 5 (45°) | 0.85 | 0.50 | 0.003 |
| | 6 (45°) | 0.85 | 0.50 | 0.003 |
| Lilly | 1 (90°) | 0.85 | 0.50 | 0.003 |
| | 2 (90°) | 0.35 | 0.50 | 0.263 |
| | 3 (45°) | 0.35 | 0.50 | 0.263 |
| | 4 (45°) | 0.70 | 0.50 | 0.115 |
| | 5 (45°) | 0.25 | 0.50 | 0.041 |
| Papu | 1 (90°) | 0.00 | 0.50 | <0.001** |
| | 2 (90°) | 1.00 | 0.50 | <0.001** |
| | 3 (45°) | 1.00 | 0.50 | <0.001** |
| | 4 (45°) | 0.15 | 0.50 | 0.003 |
| | 5 (45°) | 0.00 | 0.50 | <0.001** |
| | 6 (45°) | 0.05 | 0.50 | <0.001** |
| Pick | 1 (90°) | 0.45 | 0.50 | 0.824 |
| | 2 (90°) | 0.95 | 0.50 | <0.001** |
| | 3 (45°) | 0.00 | 0.50 | <0.001** |
| | 4 (45°) | 1.00 | 0.50 | <0.001** |
| | 5 (45°) | 0.00 | 0.50 | <0.001** |
| Plume | 1 (90°) | 0.45 | 0.50 | 0.824 |

| | | | | |
|---|---|---|---|---|
| | 2 (90°) | 0.90 | 0.50 | <0.001** |
| | 3 (45°) | 0.85 | 0.50 | 0.003 |
| | 4 (45°) | 0.45 | 0.50 | 0.824 |
| | 5 (45°) | 0.40 | 0.50 | 0.503 |
| Roku | 1 (90°) | 0.95 | 0.50 | <0.001** |
| | 2 (90°) | 0.00 | 0.50 | <0.001** |
| | 3 (45°) | 0.40 | 0.50 | 0.503 |
| | 4 (45°) | 1.00 | 0.50 | <0.001** |
| | 5 (45°) | 0.15 | 0.50 | 0.003 |
| Sunny | 1 (90°) | 0.00 | 0.50 | <0.001** |
| | 2 (90°) | 0.50 | 0.50 | 1.000 |
| | 3 (45°) | 0.00 | 0.50 | <0.001** |
| | 4 (45°) | 1.00 | 0.50 | <0.001** |
| | 5 (45°) | 0.00 (4) | 0.50 | 0.125 |
| Willy | 1 (90°) | 0.00 | 0.50 | <0.001** |
| | 2 (45°) | 0.55 | 0.50 | 0.824 |
| | 3 (45°) | 1.00 | 0.50 | <0.001** |
| | 4 (45°) | 1.00 | 0.50 | <0.001** |
| Group | 1 (90°) | 0.44 | 0.50 | 0.068 |
| | 2 (90°) | 0.57 | 0.50 | 0.056 |
| | 3 (45°) | 0.51 | 0.50 | 0.840 |
| | 4 (45°) | 0.29 | 0.50 | <0.001** |
| | 5 (45°) | 0.46 | 0.50 | 0.576 |
| | 6 (45°) | 0.57 | 0.50 | 0.193 |

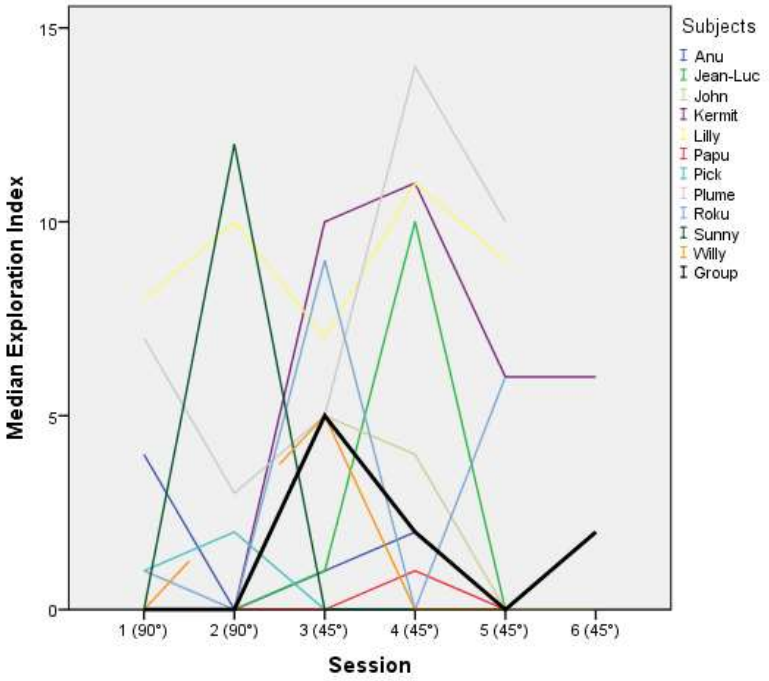



Figure 6.15 – Median Exploration Index across sessions. The black line includes data for all kea across all sessions.

### 6.9.2 Discussion

Stage 5.3 was performed to determine if the orientation of the T-maze influenced subjects' chosen arm. All but three kea displayed a preference for the left arm in two sessions when the T-maze was rotated 90°. Low EI values at the group level indicated that the T-maze's new orientation influenced side bias.

A setup difference in the 90°-rotated T-maze was that the left arm was now near the mesh wall dividing the waiting and testing areas. This suggested that social contact did not confound side preference in previous Stages but proximity to enclosure walls. Research on primates (Ross and Lukas, 2005) has shown that subjects spent more time located near dividers, doorways, and solid walls. Most of the subjects' perching and resting sites were placed near enclosure walls and dividers. It is possible that kea showed an affinity to be near these structures.

To further test if arm preference was associated with the location of walls, the T-maze was rotated 45°. In this condition, both walls (mesh divider between compartments and solid divider with the main enclosure) were equally distant to the T-maze's entry point. Five kea showed preferences for the right arm, four for the left arm, and two did not prefer either. At the group level, side preferences were less established when compared to the T-maze at 0° and 90°. EI was also lower in this setup. Extra-maze characteristics appeared to affect kea's choices. There is limited information on how environmental parameters beyond the actual T-maze affect alternation behaviour and the present methods did not allow discussion to depart from T-maze orientation.

However, it is also possible that individual differences affected kea's choices. Possenti et al. (2016) discussed the possibility of sex influencing lateralised behaviour, commenting on the role of hormones (e.g. testosterone), but their own data did not show evidence of an influence of testosterone on gull (*Larus michahellis*) chicks behaviour. Work with budgerigars (*M. undulatus*, Schiffner and Srinivasan, 2013) showed that subjects displayed lateralisation that varied between individuals with respect to a specific task: "choice of perch, landing location, or direction of approach whilst landing". In accordance to the present study, where lateralised subjects changed their preferred T-maze arm when the apparatus was rotated, data from Schiffner and Srinivasan (2013) showed that lateralisation changed its polarisation with slight task changes, (but see Vince, 1964 and Izawa et al., 2005 for contradicting evidence). Schiffner and Srinivasan (2013), however, failed to provide a reason as to why this individual preference appeared besides their association with different tasks.

## 6.10 Overall analysis

Table 6.12 shows binomial test statistics for proportion of chosen difficult tasks for each subject with all trials pooled together. Four outliers were detected when calculating the binary logistic regression for chosen difficulty. These data had a residual range of [-2.735, -2.552] and were kept in the analysis. The model predicting chosen difficulty (easy or difficult) using subject, session, trial, arm containing the difficult task, T-maze rotation, difficulty of difficult task and time of testing was statistically significant $\chi^2(17)=569.716$, $p<0.001$. However, the model had poor fit as determined by Homser and Lemeshow test ($\chi^2(8)=74.742$, $p<0.001$). The regression predicted 17.5% of the variance (Nagelkerke $R^2$). The model correctly classifies 66.5% of all cases. Sensitivity for difficult task choices was 75.4%; specificity was 54.8%. Positive predicted value was 68.5% and negative predicted value was 63.2%. Subject, Session number, Location of the difficult task in the T-maze, T-maze orientation and Time of testing were significant predictors of chosen difficulty (Table 6.13). The Subject predictor indicated that five kea had significantly higher probabilities of choosing difficult tasks. Kea were predicted to be: significantly less likely to choose a more difficult task in later sessions, significantly less likely to choose the difficult task when it was presented in the right T-maze arm, significantly less likely to choose the difficult task when the T-maze was rotated 45°, significantly less likely to choose the difficult task when a more difficult level was used, and significantly less likely to choose the difficult task during the second testing period (after eight months).

Table 6.12 – Binomial test results for proportion of choices for the difficult task for all trials. **indicates significance according to p<0.003 (corrected level).

| Kea | Total trials | Observed Proportion | Expected proportion | p |
|---|---|---|---|---|
| Anu | 300 | 0.61 | 0.50 | <0.001** |
| Jean-Luc | 480 | 0.59 | 0.50 | <0.001** |
| John | 475 | 0.57 | 0.50 | 0.002** |
| Kermit | 300 | 0.63 | 0.50 | <0.001** |
| Lilly | 460 | 0.43 | 0.50 | 0.002** |
| Papu | 350 | 0.69 | 0.50 | <0.001** |
| Pick | 280 | 0.56 | 0.50 | 0.064 |
| Plume | 378 | 0.70 | 0.50 | <0.001** |
| Roku | 280 | 0.60 | 0.50 | 0.001** |
| Sunny | 403 | 0.40 | 0.50 | <0.001** |
| Willy | 375 | 0.51 | 0.50 | 0.757 |

Table 6.13 – Binomial logistic regression predicting for pooled data.

| | B | S.E. | Wald | Degrees of freedom | p | Exp(B) | 95% C.I.for EXP(B) | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | Lower | Upper |
| Subject | | | 85.293 | 10 | <0.001 | | | |
| Subject(1) | 0.075 | 0.175 | 0.183 | 1 | 0.669 | 1.078 | 0.765 | 1.519 |
| Subject(2) | 0.681 | 0.148 | 21.131 | 1 | <0.001 | 1.976 | 1.478 | 2.641 |
| Subject(3) | 0.548 | 0.148 | 13.694 | 1 | <0.001 | 1.730 | 1.294 | 2.312 |
| Subject(4) | 0.103 | 0.185 | 0.307 | 1 | 0.580 | 1.108 | 0.771 | 1.592 |
| Subject(5) | 0.047 | 0.149 | 0.099 | 1 | 0.753 | 1.048 | 0.782 | 1.404 |
| Subject(6) | 0.448 | 0.170 | 6.948 | 1 | <0.001 | 1.565 | 1.122 | 2.183 |
| Subject(7) | -0.314 | 0.187 | 2.816 | 1 | 0.093 | 0.731 | 0.507 | 1.054 |
| Subject(8) | 0.633 | 0.163 | 15.048 | 1 | <0.001 | 1.883 | 1.368 | 2.592 |
| Subject(9) | -0.110 | 0.187 | 0.343 | 1 | 0.558 | 0.896 | 0.621 | 1.294 |
| Subject(10) | -0.178 | 0.152 | 1.375 | 1 | 0.241 | 0.837 | 0.621 | 1.127 |
| Session | -0.133 | 0.018 | 54.475 | 1 | <0.001 | 0.876 | 0.845 | 0.907 |
| Trial | 0.008 | 0.006 | 1.984 | 1 | 0.159 | 1.008 | 0.997 | 1.020 |
| Location of difficult task(1) | -1.164 | 0.069 | 282.153 | 1 | <0.001 | 0.312 | 0.272 | 0.358 |
| T-maze orientation | | | 20.041 | 2 | <0.001 | | | |
| T-maze orientation(1) | 0.070 | 0.151 | 0.214 | 1 | 0.644 | 1.072 | 0.797 | 1.442 |
| T-maze orientation(2) | -0.525 | 0.143 | 13.552 | 1 | <0.001 | 0.592 | 0.447 | 0.782 |
| Difficult task mode(1) | -0.834 | 0.140 | 35.470 | 1 | <0.001 | 0.434 | 0.330 | 0.571 |
| Time of testing(1) | -1.061 | 0.139 | 58.099 | 1 | <0.001 | 0.346 | 0.264 | 0.455 |
| Constant | 2.740 | 0.379 | 52.397 | 1 | <0.001 | 15.492 | | |

For the linear regression predicting Exploration Index, there was independence of residuals, as assessed by a Durbin-Watson statistic of 1.141. Linearity and homoscedasticity were verified by analysis of the Studentized Residual and Unstandardized Predicted Value scatterplot. Inspection of Tolerance Values indicated that there was no evidence of multicollinearity (Tolerance Value>0.1). No outliers were found in the analysis. The regression model significantly predicted EI $F(6, 196)=4.822$, $p<0.001$, adjusted $R^2=0.102$. Session number and Difficult task mode added significantly to the prediction. Table 5.14 presents predictor coefficients, standard errors, and significance levels. Kea were found to be significantly less likely to explore a different T-maze arm in later sessions and significantly

less likely explore a different T-maze arm in later sessions when a more difficult task was implemented.

Table 6.14 – Multiple linear regression predicting Exploration Index. *indicates significance according to p<0.05.

| | Unstandardized Coefficients | | Standardized Coefficients | t | p | 95.0% Confidence Interval for B | |
|---|---|---|---|---|---|---|---|
| | B | Std. Error | Beta | | | Lower Bound | Upper Bound |
| Constant | 8.491 | 1.644 | | 5.166 | <0.001* | 5.249 | 11.732 |
| Subject | 0.069 | 0.094 | 0.049 | 0.736 | 0.462 | -0.116 | 0.255 |
| Session | 0.394 | 0.093 | 0.534 | 4.218 | <0.001* | 0.210 | 0.578 |
| T-maze orientation | -0.695 | 0.590 | -0.118 | -1.178 | 0.240 | -1.857 | 0.468 |
| Location of difficult task | 0.187 | 0.602 | 0.021 | 0.310 | 0.757 | -1.000 | 1.373 |
| Difficult task mode | -3.889 | 0.992 | -0.430 | -3.920 | <0.001* | -5.845 | -1.932 |
| Time of testing | -1.246 | 0.939 | -0.131 | -1.326 | 0.186 | -3.098 | 0.607 |

## 6.11 General Discussion

This study measured captive kea's choices for varying difficulty levels. To achieve this, kea were first trained to identify a specific image as a rewarded cue. Afterwards, kea were provided with different task variations (e.g. including more non-rewarded images, changing their colour and position) to determine their difficulty levels based on the number of errors (i.e. choices for non-rewarded stimuli). From this task pool, two were selected as the easy and difficult tasks and were simultaneously provided in a T-maze arena to determine if kea preferred accessing and solving a low or high-difficulty task. This is the first study in which a parrot species is tested on challenge preference and in a T-maze arena.

One of the reservations about the T-maze is that kea could refuse to navigate it due to the smaller size of the arena when compared to their living quarters. To minimise this possibility, many studies run habituation sessions in which the T-maze is available for the subjects to explore (e.g. Arnold and Hemsworth, 2013). These familiarisation sessions were not performed to prevent side biases from establishing, as this had been observed in previous experiments with these kea (Schwing, pers. comm.). Instead, training sessions where one T-maze arm was blocked and the other was unblocked were run. This allowed subjects to obtain information about both T-maze arms in a controlled way.

This study was conducted in two phases separated by eight months, which could have confounded the results. Research on budgerigars (*M. undulatus*) showed that females remembered the call of a preferred male for at least one month after separation but this preference was extinguished after six months (Eda-Fujiwara et al., 2011), suggesting the eight-month gap in this study could have been detrimental. However, research on ravens (*C. corax*) and chimpanzees (*Pan troglodytes*) offer a different perspective, as ravens were able to differentiate the calls of familiar and unfamiliar conspecifics for up to three years (Boeckle and Bugnyar, 2012) and chimpanzees re-tested in a discrimination task after 6 months and after 3.25 years were able to solve it (Beran, 2004). In the present investigation, kea were re-tested after the eight months and they performed with low success rated in the difficult task, indicating that difficulty had been maintained but kea became more proficient at solving tasks after one session, suggesting that the time gap was not detrimental.

To interpret the results of this chapter as preferences, kea should have been aware of the difficulty contrast and of the association between T-maze arm and tasks and responded accordingly. Metacognition is the "ability to monitor one's own cognitive processes" (Perry and Barron, 2013). In human psychology, metacognition indicates that when facing uncertainty (e.g. lack of knowledge or memory), subjects will suppress responses and look for help or more information (Smith and Beran, 2009). Research on animal cognition has tried to assess if animals possess metacognition. Smith and colleagues (1995) trained one bottlenose dolphin *(Tursiops truncatus*) to respond to two different acoustic cues: one with a fixed frequency (i.e. certain) and another with a frequency range (i.e. uncertain). The dolphin was also trained to terminate the test to receive a new test with reduced difficulty. The dolphin was able to predict difficult tasks and decline them (task avoidance was determined by hesitation and wavering behaviours). Shields and colleagues (1997) trained two rhesus monkeys (*Macaca mulatta*) to classify two visual cues as same or different based on pixel density. The -different- tasks were automatically adjusted to become more difficult as subjects' performance improved, and monkeys actively declined to engage with indeterminate stimuli. Couchman and colleagues (2010) trained rhesus monkeys in sparse-dense (visual) discrimination that varied qualitatively: cues became longer/shorter or more/less rounded), with monkeys declining to solve uncertain task variations. These results showed that monkeys were able to identify difficult stimuli (Smith et al., 2009). Perry and Barron (2013) tested honeybees (*Apis mellifera*) to solve two visual discrimination tasks. Experimenters manipulated the difficulty contrast between the tasks and analysed the bees' behavioural responses, showing that bees avoided difficult tasks more compared to easy tasks.

The results from this chapter contradicted these metacognition studies as some kea showed a preference to access a difficult task. Looking at pooled data for all trials, nine subjects displayed a significant preference for one difficulty level: seven for the difficult task and two for the easy task, and two kea did not show a significant preference for either task. This study assumed that kea made a conscious choice when tested in the T-maze, that is, kea understood that one arm led to one task and the other to a more difficult level of the task. The present methodology did not allow to investigate if kea had this understanding. According to the metacognition literature, if kea had awareness of one task being difficult and they did not prefer it, they would have avoided it (i.e. choose the alternative arm). The regressions predicting choices for the difficult task and exploration of the T-maze showed that these two variables were predicted to decrease when the more difficult level of the task was provided. These results can be interpreted in two ways: kea found both tasks equally difficult (or easy) and had no need to change their choice, or kea simply did not show aversion towards the difficult task. Further experiments need to be conducted to elucidate kea's metacognition.

This study does not qualify as a contrafreeloading experiment for two reasons: 1) contrafreeloading definitions (e.g. Inglis et al., 1997) rely on providing free and non-free food. Here, the two options to obtain food required solving a visual discrimination task, it was assumed that both food sources were non-free rewards; 2) published literature on contrafreeloading relied on tasks involving a strong physical component: giraffes foraging from troughs or "challenging grain feeders" (Sasson-Yenor and Powell, 2019); pigeons retrieving free grains vs. grains buried in sand (Anselme et al., 2018); food in a tray vs. food dispersed in the enclosure of maned wolves (Vasconcellos et al., 2012); continually playing films vs. playback requiring macaque (*Macaca fuscata*) responses (Tadatoshi, 2011); providing frozen food vs. food in boxes vs. free food to grizzly bears (*Ursus arctos horribilis*; McGowan et al., 2010) and kea manipulating rocks and wooden blocks or lids, corks and membranes to obtain a food reward (Chapters 4 and 5 of the present thesis). The results from this Chapter provide information on captive animals' choices in a cognitive framework.

## 6.12 Conclusions

- Kea were able to discriminate visual cues and learned to associate one image as a rewarded stimulus.

- Kea required more sessions to reach criteria and had lower success rates when "noise" (number of non-rewarded images) was increased on the positive and negative stimuli, indicating an increased difficulty level.

- Kea were able to navigate a T-maze and engage with a discrimination task. The orientation of the T-maze in respect to the testing compartment had an influence in chosen T-maze arm.

- A learning effect was found based on the success rates of the difficult task: kea's performance increased to levels comparable to the easy task. When the difficult task was replaced with a more difficult level, the difficulty contrast increased as success rates decreased.

- Overall, subjects accessed the T-maze arm containing the difficult task more often. However, some subjects showed a strong side bias by always choosing the same T-maze arm, irrespective of what task it contained.

# Chapter 7. General Discussion

## 7.1 Summary

The work presented in this thesis stems from the researcher's interest in providing captive kea with adequate living environments. For this, four general objectives were followed:

***1) Obtaining information on the status quo of the management, husbandry and behaviour of captive kea and appraise these in terms of well-being (Chapter 2)***.

***2) Evaluating specific management / husbandry practices in terms of behaviour-based well-being (Chapters 3 and 4).***

***3) Determining if captive kea contrafreeload (Chapters 4 and 5).***

***4) Investigating captive kea's choices as a precursor for preference and motivation-based well-being (Chapters 5 and 6).***

Specifically, in Chapter 2, an online survey was developed and distributed amongst kea-holding institutions worldwide to obtain information on captive kea's demographics, management, and general behaviour. The results from this Chapter showed which methods were reported to be common and uncommon enrichment protocols, as well as provide a general indication of the occurrence of specific behaviours in the surveyed captive kea population that are frequently associated with poor well-being in captive parrots.

In Chapter 3, an experiment was developed to determine if captive kea behaviour changed due to sensory stimulation and to thereby evaluate the potential of this protocol as enrichment. Choosing sensory stimulation as the enrichment type came as a result of Chapters 1 and 2 showing that this type of stimulus was the least commonly reported to be used as parrot/kea enrichment and previous research showing the potential of sensory stimulation in terms of positive well-being (reviewed in Chapter 3.1).

In Chapter 4, an experiment was developed where a foraging manipulation was introduced to a group of captive kea and their foraging behaviours with and without the manipulation were compared, expecting to see foraging patterns aligned with that of wild kea. Also, evidence for contrafreeloading behaviour was obtained, indicating that kea could have an intrinsic drive to display species-specific behaviours such as foraging and exploration (see Chapters 1.2.5 and 4.1).

Chapter 5 was performed as a follow-up to Chapter 4, as kea performed contrafreeloading, but did not show a significant preference to perform this behaviour. Due to the limitations of Chapter 4 (explained in Section 7.3), another foraging task was developed

in which specific task-related variables were manipulated to determine what might increase the expression of contrafreeloading behaviour in terms of foraging choices.

Chapter 6 followed a novel approach towards enrichment in terms of cognitive performance. Following the literature on large-brained mammals who engage in complex, cognitive tasks and whose well-being appears to be positively impacted (e.g. Clark, 2013), captive kea were trained to solve a visual discrimination task with varying difficulties to investigate which levels involved higher difficulties (measured based on subjects' success rates when solving the discrimination task) and if kea preferred engaging with a difficult (more challenging) or easy (less challenging) level.

## 7.2 Discussion of main findings

This research intended to fulfil a set of general objectives that were introduced in Chapter 1 along with specific questions that were detailed in each experimental chapter (Chapters 2, 3, 4, 5 and 6). The answers to these specific questions are presented next.

### 7.2.1 What are the current management protocols for captive kea around the world?

By developing and distributing an online survey to kea holders around the world, data were collected on 77% (N=190) of the reported kea population in 2015. The most frequent kea enclosure housed more than one individual, with most cases being pairs. The most frequent foraging schedule consisted of two feedings per day. The enrichment schedule for captive kea was mostly based on a daily provision, with foraging and physical stimulation being the most frequent types of enrichment. These results coincide with the recommendations provided in the kea husbandry manual (Orr-Walker, 2010), which are suggested as guidelines to ensure the well-being of captive kea but are not backed with scientific evidence.

### 7.2.2 What is the occurrence of abnormal behaviours (recognised in captive parrots) in the captive kea population?

The review presented in Chapter 1 identified specific abnormal behaviours in captive parrots that develop or increase in suboptimal captive conditions and are used as well-being indicators, namely feather damaging behaviour, stereotypies, and health and reproduction problems. The online survey therefore included a section asking to report if any kea performed pacing behaviour, feather damaging behaviour or abnormal reproduction.

Abnormal reproduction was reported in 11% of surveyed kea. Feather damaging behaviour was reported in 2.5% of the surveyed kea. Pacing behaviour was reported in 17% of the surveyed kea, similar to the occurrence reported by Orr-Walker (2005) in a smaller group of captive kea in New Zealand but contrasting with the 96% of captive amazons (*Amazona amazonica*) reported to perform locomotor and/or oral stereotypies in a private colony (Meehan, 2002).

### 7.2.3 Do husbandry and management practices correlate with the occurrence of abnormal behaviours of captive kea?

Chapter 1 evidenced how captive environments may negatively impact the well-being of captive animals by being under-stimulating, non-naturalistic, and not allowing the expression of certain behaviours. The kea husbandry manual (Orr-Walker, 2011) provides recommendations based on the assumption that certain characteristics of the physical (captive) environment and specific husbandry practices should positively impact kea well-being. While these recommendations seem acceptable based on research on other parrot species (see Chapter 1, Table 1.2), there is no kea-based research to support them nor have they been evaluated to determine their effectiveness.

Data on captive kea husbandry and management were used to create input variables for regression analyses predicting the proportion of kea per enclosure engaging in abnormal behaviours. Feather damaging was the only behaviour found to be significantly predicted by the regression analysis, with a positive correlation with the “Feeding Frequency” predictor. This result contradicts existing literature on feather damaging behaviour, as increased foraging opportunities have been reported to reduce and prevent feather damaging behaviour (e.g. Meehan et al., 2013b). The interpretation for this result is that increasing foraging opportunities was performed as a counter or preventative measure for feather damaging behaviour.

### 7.2.4 Does exposure to sensory stimuli affect the behaviour of captive kea? Is this indicative of a well-being impact?

Chapters 1 and 2 found that sensory-based enrichment is the least frequent type provided to captive parrots and kea with no indication as to why. There is evidence that sensory stimulation on other bird species results in behavioural changes interpreted as a positive well-being effect (reviewed in Chapter 3). Chapter 3 implemented a sensory-based protocol to determine if kea well-being was enhanced by it.

Providing kea with sensory stimulation in the form of video and audio playback influenced their behavioural repertoire. Chewing wire (i.e. enclosure walls), drinking, object manipulation and preening behaviours were shown to be significantly different across the five experimental phases (baseline, naturalistic sounds, naturalistic videos, non-naturalistic sounds, and non-naturalistic videos).

Drinking behaviour was discussed as being significant only because of its low/null observations but the remaining behaviours were discussed in terms of well-being. Preening behaviour duration increased when kea were exposed to naturalistic stimuli. Increases in preening behaviour may be interpreted as either evidence for or against good well-being. If preening occurs at high rates they could develop into abnormal behaviours (e.g. feather plucking, van Zeeland et al., 2009). The most likely interpretation of this change in preening behaviour, based on the lack of historic feather damaging behaviour on the subjects and post-experimental, anecdotal observations, is that kea were displaying an essential behaviour (as it maintains skin and feathers; van Zeeland et al., 2009; Kubiak, 2015) that has also been associated with a calmed state (Williams et al., 2017). Chewing wires, a behaviour associated with negative well-being (Meehan et al., 2004) decreased from baseline levels in all conditions except for naturalistic videos. As with preening behaviour, the increased expression of chewing wires during naturalistic videos could be interpreted as a negative well-being effect in terms of heightened frustration, for example. Finally, the duration of object manipulation increased in all phases apart from when naturalistic sounds were presented. This result may be considered as a positive impact on well-being as kea were displaying a natural behaviour (exploration, see Diamond and Bond, 1999) that has been associated with behaviour-based well-being (e.g. Meehan and Mench, 2002).

Overall, the results of Chapter 3 allow to classify sensory stimulation as enrichment, given the behavioural modifications, which align with functional and natural-living frameworks of well-being explained in Chapter 1. Furthermore, these results are promising from a management perspective, as providing audio-visual stimuli can be done with minimal work from the caretakers' side (e.g. just providing access to a speaker or display) and could expand on institutions' enrichment repertoire.

### 7.2.5 Does a change in food presentation affect the foraging behaviour of captive kea?

When captive kea were given the option to forage from a tray containing free-to-access food and a tray with food covered by objects, foraging behaviour duration was comparable across both options, indicating that the intervention did not have any significant effect. While not significant, foraging duration was greater when wooden blocks than when

rocks were used as covering objects or when no objects were added to either tray. When analysing the physical interactions between kea and the added objects, kea interacted more (albeit non-significantly) with the wooden blocks than with the rocks. The results from Chapter 3 seem to indicate that the intervention did not have any enrichment effect based on foraging durations. Nonetheless, as kea still foraged from both trays (with and without objects), this protocol could still be implemented to minimise the commonplace practice of feeding captive animals in simplistic and non-naturalistic ways (e.g. processed food in trays) that have been shown to constrain the expression of natural, foraging behaviours (e.g. Shepherdson et al., 1993). Additionally, there was evidence of play behaviour being displayed with the wooden blocks and not with the rocks, which warrants further research.

### 7.2.6 Do kea contrafreeload?

When captive kea were given the option to forage from a tray containing free-to-access food and food covered by objects in Chapter 4, they were found to forage from both trays. The fact that they would also forage from trays which require some work to access the food when free food was available elsewhere suggests contrafreeloading behaviour was performed (Inglis et al, 1997). However, when analysing first chosen tray and foraging durations at each of the two tray options, kea were shown to have no tray preference.

The results of Chapter 5 similarly provided demonstration of contrafreeloading behaviour in captive kea, as subjects were given a foraging board where food rewards were either uncovered (i.e. free-to-access) or covered. While there was a preference to retrieve uncovered rewards first, kea still contrafreeloaded as they retrieved covered rewards when uncovered rewards were still available.

These results agreed with thesis predictions based on kea's exploration and neophilia (Diamond and Bond, 1999). Results are relevant following the rationale provided by Špinka and Wemelsfelder (2011), who discuss how animals are motivated to explore and thus contrafreeload. It is proposed that opportunities to perform behaviours related to contrafreeloading, such as exploration, may promote their well-being in captivity.

### 7.2.7 Do kea show a preference for specific manipulanda during a foraging task?

In Chapter 5, the sequence of choices for covered and uncovered rewards were compared across three manipulandum options, in addition with physical and visual access of the food reward. Comparisons between all three types of manipulandum showed that kea preferred to obtain food rewards by interacting with membrane-like structures requiring being ripped off more than lids requiring being rotated and corks requiring being lifted. Also, when

transparent and opaque versions of each manipulandum were provided and kea could obtain free or non-free food rewards, kea showed a weak contrafreeloading (i.e. preferring to access free food in earlier choices) with opaque manipulanda.

### 7.2.8 Do kea engage in visual discrimination tasks of varying difficulty? Is a specific difficulty level preferred?

Kea were trained on a visual discrimination task where they had to identify one image as the positive cue. Several levels saw an increase in the number of negative cues (different shapes and colours). Kea successfully learned the task and only struggled to discriminate when there were many negative (i.e. non indicative of a reward) cues and when the cues' colour was uniform (red). When kea could choose a difficult or an easy level of the task in a T-maze, there was a side bias, as half of the subjects consistently chose the right T-maze arm. The subjects that did not show this bias showed individual differences in their preferred task. At the group level, kea entered the T-maze arm with the difficult task more frequently.

## 7.3 Methodological strengths and weaknesses

### 7.3.1 Sample sizes

The first general shortcoming of this research project pertains to sample sizes. The number of animals kept in captivity depends on many variables including space availability, species' natural history and stock availability; many species are kept as female-male pairs and their offspring (Kuhar, 2006). Zoo-based research must deal with these restrictions, often resulting in small sample sizes.

During the planning stage of this research project, captive kea populations were identified across the UK. Initially, this research project had proposed the captive kea group at Bristol Zoo Gardens as subjects for all experiments (the group was originally conformed by seven kea but later on it would be reduced to only two, this change was not known or expected by the researcher) and, under such declaration, the experiment described in Chapter 4 (the first experiment from the research project's timeline) worked with this kea group.

Paradise Park (Hayle, UK) was the institution with the largest kea group in the UK, with 13 kea. Using these as study subjects would yield the greatest test sensitivity to treatment effects. The researcher visited Paradise Park to discuss the possibility of performing part of his research there, which was agreed upon. After relocating to Cornwall to start the experiment discussed in Chapter 3, the researcher identified that kea were kept in the park with contrasting housing conditions: one group of 4 kea housed with other parrot

species in a large, public enclosure. All but one of the remaining kea were housed as male-female pairs in off-show enclosures. It would have proven difficult to obtain comparable data from all kea given their contrasting enclosures, housing conditions, visitor access, and social environment. Group-housed kea were not part of the experiment in Chapter 3 due to said confounds in addition to complicating the delivery of sensory stimuli (playback devices would have had to be left in areas accessible by the public). Even after removing the four kea from the study, nine kea still proved to be a higher number than the next largest kea group in the UK.

The possibility of working at the “Kea Lab” in Vienna, with the largest captive kea group (Chapters 5 and 6), was facilitated by the researcher’s new secondary supervisor after the doctoral programme had already started and the experiments in Chapters 3 and 4 were already planned and agreed upon.

### 7.3.2 Chapter 2

In Chapter 2, a survey was designed and distributed to obtain husbandry and behavioural information on captive kea. Descriptive behavioural research on a large proportion of a captive population represents information useful to guide and define breeding and management programmes (Hosey, 1997). Surveys are popular instruments to obtain data on large numbers of institutions and individuals (Rowden and Rose, 2016; Haspeslagh et al., 2013; Fuller et al., 2013; Bashaw et al., 2001). The survey was circulated to all institutions listed on the “Species Holding Report”. However, since there was no specific contact information available on this report, it had to be obtained from the internet. While looking at the institutions’ website, the researcher tried to locate the contact information of the curator of the bird section (or any homologous position), as it was thought they would readily reply to the survey. Not all zoos listed this information, and many had to be contacted via a general form or email and then redirected to the appropriate contact. This resulted in a heterogenous list of job titles answering the survey, including curators, zookeepers, research staff and veterinarians (the survey included a question to identify the respondent’s position). Ideally, survey respondents should have been the regular caretakers, as they observe animals and their behaviour the most. A way to minimise the effect of respondents with differential experience with kea was to include a limited number of open questions and a larger number of multiple-choice questions.

The survey asked for information on six behaviours, three associated with negative well-being (pacing, feather-picking and abnormal reproduction) and three not associated with negative well-being (social play, tool use and hanging from the beak). A shortcoming of the

survey was that it only provided definitions for the three behaviours associated with negative well-being.

Feather damaging behaviour can be easily detected in many parrot species (Chitty, 2003a) as in most cases the behaviour or its consequences (e.g. featherless patches) can be directly observed. Pacing was defined in the survey as “moving in constant, fixed patterns”. Pacing behaviour has been observed and studied in a variety of taxa (see Rose et al., 2017 for a review). The public even recognises pacing as a behavioural problem common to zoo animals. For example, a quick search on YouTube for “pacing animals” returns videos (with thousands of views) of captive carnivores engaging in this abnormal repetitive behaviour (Figure 7.1). Survey respondents are assumed to be more knowledgeable in terms of animal behaviour than the public, thus being able to identify pacing as a stereotypical behaviour and its performance by animals in their care. Based on this premise, their reports on the occurrence of pacing behaviour in the captive kea population would be correct but in its current state, the data from Chapter 2 do not allow to establish this conclusion.

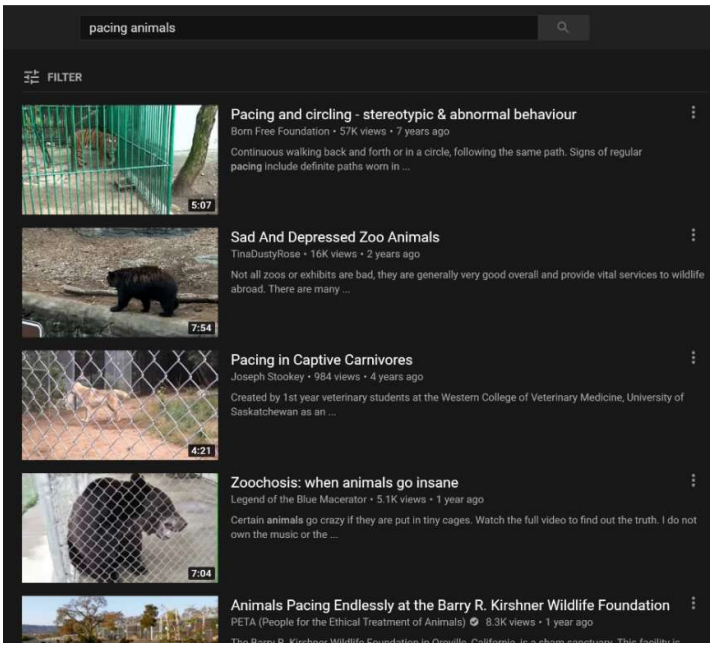



Figure 7.1 – The first four results after searching on YouTube for “pacing animals” without any filters. All videos display animals performing stereotypic locomotion / route-tracing. Results appear biased towards mammalian species.

Another possible confounding factor for the survey results is the relocation of kea to different enclosures. It is common for zoos to transfer their stock to a different enclosure as part of their management practices. The researcher noticed three instances of kea

relocations during convenience zoo visits. In one location, kea were maintained as a group outside of the breeding season. During the breeding period, pairs were formed and housed separately in different enclosures. In a second location, keepers reported the death of several kea due to lead poisoning from metallic fixtures in the enclosure, and the remaining kea had to be relocated. A third zoo was undergoing renovations and a new, improved kea enclosure was being built. Kea had to be housed in a smaller, temporary enclosure during these renovations. In this case, kea behaviours could have been influenced by previous living quarters and not by the ones being described. Well-being studies on non-avian taxa have shown that enclosure relocation impacts behaviour and physiology. An Asian elephant (*Elephas maximus*) transferred to a new herd showed a 400% increase in both cortisol metabolite excretion and stereotypical behaviour following the relocation (Laws et al., 2007). Rhesus monkeys *(Macaca mulatta)* infants showed increases in hair cortisol levels and anxious behaviour after a relocation event and these effects were shown to persist up to sixteen months post-relocation (Dettmer et al., 2012). While it is not known which are the well-being effects (either positive or negative) of kea relocation to different enclosures, a survey item asking for any relocations happening in the past could have controlled for this possibility.

### 7.3.3 Chapter 3

A weakness of this Chapter relates to the devices presenting stimuli used as putative enrichment. Audio and video files were played on two devices: a tablet and a larger convertible laptop. Device differences could influence the stimuli delivery or perception. To control for the possibility of differential device effects, each kea was always exposed to stimuli being played on the same device.

As reviewed in Chapter 3.1, studies providing sensory stimulation have not followed a systematic approach in terms of provided cues and measured behaviours to perform an enrichment assessment. The experiment in Chapter 3 improved upon these protocols, as it provided auditory and visual stimuli, each with a naturalistic and a non-naturalistic modality and included a behavioural analysis was with an ethogram including general behaviours.

### 7.3.4 Chapter 4

One of the questions this Chapter attempted to answer was if kea contrafreeloaded. There are only three studies referring to the contrafreeloading phenomenon with psittacine subjects. showing contrasting results (see Chapter 4). In two of these studies, contrafreeloading was assessed opportunistically, as it was not in their aims to determine if subjects contrafreeloaded or not. This thesis would present the second formal study on

psittacine contrafreeloading, though the first study (Van Zeeland et al., 2010) was presented in a conference and is not available as a published manuscript.

This experiment was performed in a zoo environment, so it was difficult to fully control for variables that could have confounded the results such as the effect of zoo visitors. The captive kea group was composed of an adult breeding pair and their three offspring. The three juvenile kea showed a tendency to forage close to the female and each other. Conversely, the adult male was often foraging away from the female. These observations indicate the possibility of a social confounding factor. Unfortunately, kea could not be separated to be tested in isolation and minimise this confounder, which complicates the generalisation of the results to the whole captive kea population.

A suggested methodological improvement could be to provide both food trays closer together, as it is possible that the original distance between food trays was interpreted by the kea as two independent foraging opportunities rather than identifying them as a choice. Performing this modification (both trays closer to each other) was not possible as advised by zookeepers as sometimes a kea would monopolise a food tray and prevent others from feeding.

### 7.3.5 Chapter 5

Many contrafreeloading studies require animals to forage for either free or non-free food from two separate feeders or locations (e.g. 4; Van Os et al., 2017; Vasconcellos et al., 2012). In Chapter 5, only one apparatus was involved to determine preferences. Kea had to access food rewards placed in holes spaced ca. 5 cm (see Figure 5.2 in Chapter 1). It could be argued that kea perceived this setup as one foraging opportunity and not as a sequence of choices with two conditions. Before providing the actual foraging task, a pilot study was conducted in which two foraging boards were provided, one containing holes with free food and the other non-free food. One wooden shape (square or triangle) was placed behind each board to act as treatment cues, assuming kea would learn that one shape was associated with one treatment. Unfortunately, kea did not learn this association. More importantly, kea displayed a side bias, choosing the board to the right during the pilot study. For this reason, the task was adapted to only using one apparatus. During experimental sessions, kea could always complete the foraging task (i.e. retrieve all food rewards), which differs from the methodologies of other contrafreeloading studies. For example, maned wolves offered food either dispersed (non-free) or in a tray (free) only managed to consume 50% of the non-free food (Vasconcellos et al., 2012). Being able to retrieve all rewards in each session could have affected the subjects' perceived contrast between the work required. In other words, the fact that kea always retrieved all covered and uncovered

rewards could dilute the choice contrast. However, baseline sessions quantifying the amount of work required to retrieve all rewards (using time to collect and eat all rewards as an indicator) had shown that retrieving covered food rewards did require significantly more work, which allowed to distinguish the free and non-free rewards and assume kea also perceived this difference.

A strength of this chapter is that it analysed the effect of several task-pertaining variables on preference responses, which is lacking in the contrafreeloading literature. Previous studies have looked at the effects on contrafreeloading by several factors. Neurobiological research has shown that dopamine affects contrafreeloading behaviour. Research on rodents has found that administering subjects with dopamine increases contrafreeloading (e.g. Frederick and Cocuzzo, 2017) but research on avian species found different results, as pigeons injected with a dopamine solution did not alter their original preference towards free food (Anselme et al., 2018). Reinforcement rate has also been shown to affect contrafreeloading, as rats contrafreeloaded more in the presence of a discriminative stimuli arranging higher reinforcement rates (Podlesnik and Jimenez-Homez, 2016). Early life adversity in the form of high nestling competition for parent-sourced food was also found to correlate with contrafreeloading, as developmentally disadvantaged starling (*Sturnus vulgaris*) chicks contrafreeloaded more than advantaged (i.e. fatter in adulthood) conspecifics (Andrews et al., 2015). Research on poultry has also identified age, sex, social isolation, domestication, and stress levels as factors correlated with contrafreeloading (Lindqvist and Jensen, 2008; 2009). This Chapter's results provide evidence on the effects of the type of work in contrafreeloading.

### 7.3.6 Chapter 6

Cognitive enrichment is defined as using cognitive skills in problem-solving or environmental-control opportunities (Clark, 2017). One of the strengths of this Chapter is that, unlike past research with other species (e.g. Puppe et al., 2007; Langbein et al., 2009), this experiment had an initial phase in which the difficulty level of each task was measured. This ensured that in testing sessions actual (i.e. previously assessed) easy and difficult tasks were used.

A two-arm T-maze was used as the arena to determine task preferences. T-mazes have been criticised as tools to measure animal behaviour (e.g. lack of reliability and validity, Tolman and Nyswander, 1927). Ideas for different apparatuses to measure challenge preference were initially brainstormed. For example, it was suggested to simply place each task at opposite ends of the compartment and allow kea to walk to either one. One limitation of this suggestion was that kea would be able to see both tasks simultaneously when

entering the compartment and it would be possible for a kea to solve both tasks before deciding on which one to attend to. Using a T-maze proved to be the simplest way for kea to choose a task without prior visual inspection of the actual tasks (and potentially solving them before choosing one). Richman and colleagues (1970) discuss how T and Y mazes predispose subjects to “attend directional cues and ignore visual stimuli”. The side bias found in some kea indicates that directional cues could be confounding subjects’ arm choice. Changes in the T-maze’s orientation were made to determine if positional cues were confounding choices, which turn out to be the case. A follow-up study in which the colour of one side of the T-maze contrasts from the other side could strengthen subjects’ association of T-maze arm with task difficulty. Another criticism of choice tests to measure preferences is that the frequency of tests can affect animal preferences (Marques Maia & Luiz Volpato, 2016). A way to minimise this limitation is by increasing the number of successive tests (Marques Maia & Luiz Volpato, 2016). This was considered in Chapter 6, as kea were tested for twenty consecutive trials per session.

## 7.4 Implications and recommendations for future research

Given that the aim of this research project is to contribute to the improvement of captive kea environments, the most important conclusion relates to how results are relevant to the keeping of kea in captivity. Data from the survey provide a descriptive overview of husbandry practices and common enrichment protocols that can be used as a reference to those interested in increasing their knowledge on captive kea management. These data also provide an initial indication of the occurrence of abnormal behaviours in the captive kea population, which have been recognised as indicators of poor well-being in other parrot species.

The protocols in Chapter 3, relying on the provision of audio-visual stimuli, were proven to enrich the housing of a group of captive kea based on behavioural measures. Chapter 2 indicated that sensory enrichment is the least used enrichment type. Chapter 3 provides evidence for utilising sensory stimulation, as it is a simple way to deliver non-food stimuli (providing kea caretakers have access to the required technology). In Chapter 3, kea were continuously exposed to music and videos during a short period of time. Thus, a further improvement on this experiment could investigate the effect of different durations. The researcher is also interested in allowing subjects to determine when and which stimuli are delivered. In other words, it would be interesting to allow kea to press a button to start/stop the delivery of specific stimuli. This protocol has been implemented only on a low number of mammalian species and have found no evidence to preferring one stimulus type (e.g. Wallace et al., 2017).

Chapters 4 and 5 investigated contrafreeloading behaviour on kea. The data collected from these two chapters demonstrate that kea do contrafreeload, which has implications for kea caretakers under the rationale that kea may possess a need to perform certain behaviours such as foraging and exploration that should be satisfied in their captive environments. Chapter 5 provides information on specific situations that favour the expression of contrafreeloading behaviour based on a foraging task. In summary, if kea are provided with a visible resource (e.g. food) requiring extraction by manipulating a membrane-like barrier, kea favour contrafreeloading. These findings are helpful when designing potential enrichment opportunities for kea to ensure animals show interest in interacting with it.

Cognitive enrichment has been proposed as a novel enrichment category (see Chapters 1 and 6) whose effects on well-being appear to be greater than those of traditional (e.g. physical) enrichment opportunities (e.g. pigeons exposed to cognitive enrichment performed less stereotypy and auto-grooming behaviour and were more optimistic than when exposed to physical enrichment in Millar, 2013). Most protocols on cognitive enrichment provide a "challenge" in the form of an operant or discrimination task but researchers do not provide a rationale or evaluate said tasks to determine how challenging they are. Following the rationale that "animals make choices that are in their own best interests" (Fraser and Mathews, 1997), it is also relevant to understand what challenge levels are preferred, both in terms of well-being effects and to ensure subjects interact with the tasks. Chapter 6 showed that the difficulty level that was initially attributed by the researcher to each task variation prior testing was not accurate, which implies that animals' may not perceive a challenge as expected and thus this evaluation phase should be performed.

Finally, this thesis does not suggest that the methods and results herein discussed are a universal panacea in terms of potentially improving the well-being of all captive animals. This thesis recognises that well-being assessments should integrate more than one indicator and/or approach to the extent that a pilot study was conducted to attempt to measure the physiological well-being of captive kea but due to limited resources it could not be expanded upon (see Appendix 4). The protocols described in Chapters 3 through 6 are just an example of the many research avenues that can be followed to provide appropriate captive environments.

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**Appendix 1. Survey questionnaire**

# Kea husbandry and enrichment

## General information

This form was created as part of my PhD research on kea enrichment and behaviour. The main objective is to collect information about the current status of kea husbandry and the use of environmental enrichment in zoos around the world. This survey should be completed by staff most familiar with the daily husbandry of the kea. Your help completing this form is greatly appreciated.

Please indicate the name of the zoo / institution / organisation you work in. * *Required*

Please indicate your name (optional), current position / role and how long you have been in that position. * *Required*

How many kea are currently in your collection? * *Required*

Are your kea housed in one or in multiple aviaries? * *Required*

## Information about aviary #1

How many kea live in this enclosure? (Juveniles: sexually immature)

| | Male * *Required* | Female * *Required* |
|---|---|---|
| Juvenile | 0 | 0 |
| Adult | 0 | 0 |

Please choose all the elements that can be found inside your aviary. * *Required*

- ☐ Trees
- ☐ Bushes
- ☐ Single rocks
- ☐ Rock formations
- ☐ Still water (pool, pond, etc)
- ☐ Running water (waterfall, stream, etc)
- ☐ Natural perching sites (branches)
- ☐ Artificial perching sites (tubes, beams)
- ☐ Nesting sites
- ☐ Toys (food dispensers)
- ☐ Toys (manipulation, destruction)
- ☐ Ropes
- ☐ Cement (flooring)
- ☐ Grass (flooring)
- ☐ Bark (flooring)
- ☐ Soil (flooring)
- ☐ Mesh walls
- ☐ Glass / acrylic walls
- ☐ Concrete / wooden walls

What type of aviary is it? * *Required*

- ○ Indoor aviary
- ○ Outdoor aviary
- ○ Includes both an indoor and outdoor section

Is this a walk-through aviary? Is the general public allowed inside? * *Required*

- ○ Yes
- ○ No

What species can be found in this aviary? * *Required*

- ○ Only kea
- ○ Kea and other birds
- ○ Kea and other species (mammals, reptiles, etc)
- ○ Kea, birds and other species (mammals, reptiles, etc)

How are the kea in this aviary fed? * *Required*

- ○ Once per day
- ○ Two times per day
- ○ Three times per day
- ○ Other

If you selected Other, please specify:

Please indicate how many kea in this aviary exhibit the following behaviours.

| | Juvenile male | Juvenile female | Adult male | Adult female |
|---|---|---|---|---|
| Pacing (moving in constant, fixed patterns) | 0 | 0 | 0 | 0 |
| Hanging by the beak from roof / branches | 0 | 0 | 0 | 0 |
| Feather picking (remove or damage feather from self) | 0 | 0 | 0 | 0 |
| Social play | 0 | 0 | 0 | 0 |
| Abnormal reproductive behaviour (redirected behaviour, early/late breeding, non-breeding) | 0 | 0 | 0 | 0 |
| Tool use | 0 | 0 | 0 | 0 |

Could you briefly describe this aviary? (Is it the regular enclosure, used for breeding purposes, medical treatment, is it off-show, are birds being trained, is it temporary?) * *Required*

Do the kea in this aviary receive enrichment? * *Required*

- ○ Yes, one time per day
- ○ Yes, several times per week
- ○ Yes, several times per month
- ○ No enrichment is provided

What types of enrichment do the kea in this aviary receive? Choose all that apply. * *Required*

- ☐ Foraging enrichment (feeding strategies)
- ☐ Sensory enrichment (sound, smell)
- ☐ Social enrichment (changes in social structure, human interaction)
- ☐ Physical enrichment (changes in the enclosure furniture / objects)
- ☐ Occupational enrichment (tasks, problems, challenges)
- ☐ No enrichment is provided

Could you mention one or two specific examples of enrichment you use the most? (For example scatter food or a specific type of puzzle feeder) * *Required*

Are there more aviaries, besides the one you just described, in which you keep kea? * *Required*

- ○ Yes
- ○ No

## Final information

Has there been any formal scientific research with the kea in your collection? (Choose all that aply) * *Required*

- ☐ Research on general kea behaviour
- ☐ Research on kea reproduction
- ☐ Research on kea abnormal behaviour
- ☐ Research on kea enrichment
- ☐ Research on kea cognition
- ☐ No sesearch has been performed
- ☐ Other

If you selected Other, please specify:

## Appendix 2. Normality tests

| | Kolmogorov-Smirnov[a] | | | Shapiro-Wilk | | |
|---|---|---|---|---|---|---|
| | Statistic | df | Sig. | Statistic | df | Sig. |
| Aggression duration (Baseline) | .519 | 9 | .000 | .390 | 9 | .000 |
| Aggression duration (Non-naturalistic sounds) | .519 | 9 | .000 | .390 | 9 | .000 |
| Aggression duration (Non-naturalistic sounds) | .467 | 9 | .000 | .569 | 9 | .000 |
| Aggression duration (Naturalistic videos) | .324 | 9 | .007 | .785 | 9 | .014 |
| Aggression duration (Naturalistic videos) | .413 | 9 | .000 | .656 | 9 | .000 |
| Affiliation duration (Baseline) | . | 9 | . | . | 9 | . |
| Affiliation duration (Naturalistic sounds) | . | 9 | . | . | 9 | . |
| Affiliation duration (Naturalistic videos) | . | 9 | . | . | 9 | . |
| Affiliation duration (Non-naturalistic sounds) | . | 9 | . | . | 9 | . |
| Affiliation duration (Non-naturalistic videos) | .471 | 9 | .000 | .536 | 9 | .000 |
| Eating duration (Baseline) | . | 9 | . | . | 9 | . |
| Eating duration (Non-naturalistic sounds) | .519 | 9 | .000 | .390 | 9 | .000 |
| Eating duration (Non-naturalistic videos) | .417 | 9 | .000 | .453 | 9 | .000 |
| Eating duration (Naturalistic sounds) | .468 | 9 | .000 | .568 | 9 | .000 |
| Eating duration (Naturalistic videos) | .307 | 9 | .014 | .589 | 9 | .000 |
| Drinking duration (Baseline) | .450 | 9 | .000 | .539 | 9 | .000 |
| Drinking duration (Non-naturalistic sounds) | . | 9 | . | . | 9 | . |
| Drinking duration (Non-naturalistic videos) | . | 9 | . | . | 9 | . |
| Drinking duration (Naturalistic sounds) | . | 9 | . | . | 9 | . |
| Drinking duration (Naturalistic videos) | .342 | 9 | .003 | .545 | 9 | .000 |
| Locomotion duration (Baseline) | .257 | 9 | .088 | .847 | 9 | .069 |
| Locomotion duration (Non-naturalistic sounds) | .249 | 9 | .115 | .837 | 9 | .053 |
| Locomotion duration (Non-naturalistic videos) | .186 | 9 | .200* | .897 | 9 | .234 |
| Locomotion duration (Naturalistic sounds) | .163 | 9 | .200* | .962 | 9 | .819 |
| Locomotion duration (Naturalistic videos) | .206 | 9 | .200* | .853 | 9 | .081 |
| Object manipulation duration (Baseline) | .330 | 9 | .005 | .542 | 9 | .000 |
| Object manipulation duration (Non-naturalistic sounds) | .403 | 9 | .000 | .461 | 9 | .000 |
| Object manipulation duration (Non-naturalistic videos) | .243 | 9 | .135 | .816 | 9 | .031 |
| Object manipulation duration (Naturalistic sounds) | .519 | 9 | .000 | .390 | 9 | .000 |
| Object manipulation duration (Naturalistic videos) | .305 | 9 | .015 | .601 | 9 | .000 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Preening duration (Baseline) | .295 | 9 | .024 | .734 | 9 | .004 |
| Preening duration (Non-naturalistic sounds) | .298 | 9 | .020 | .678 | 9 | .001 |
| Preening duration (Non-naturalistic videos) | .356 | 9 | .002 | .535 | 9 | .000 |
| Preening duration (Naturalistic sounds) | .348 | 9 | .002 | .631 | 9 | .000 |
| Preening duration (Naturalistic videos) | .175 | 9 | .200* | .922 | 9 | .410 |
| Resting duration (Baseline) | .233 | 9 | .172 | .818 | 9 | .033 |
| Resting duration (Non-naturalistic sounds) | .291 | 9 | .027 | .828 | 9 | .043 |
| Resting duration (Non-naturalistic videos) | .225 | 9 | .200* | .896 | 9 | .232 |
| Resting duration (Naturalistic sounds) | .238 | 9 | .148 | .916 | 9 | .358 |
| Resting duration (Naturalistic videos) | .362 | 9 | .001 | .780 | 9 | .012 |
| Attentive to device duration (Baseline) | .192 | 9 | .200* | .931 | 9 | .493 |
| Attentive to device duration (Non-naturalistic sounds) | .173 | 9 | .200* | .915 | 9 | .356 |
| Attentive to device duration (Non-naturalistic videos) | .167 | 9 | .200* | .926 | 9 | .447 |
| Attentive to device duration (Naturalistic sounds) | .252 | 9 | .104 | .877 | 9 | .145 |
| Attentive to device duration (Naturalistic videos) | .145 | 9 | .200* | .940 | 9 | .578 |
| Climbing duration (Baseline) | .252 | 9 | .102 | .848 | 9 | .070 |
| Climbing duration (Non-naturalistic sounds) | .198 | 9 | .200* | .913 | 9 | .334 |
| Climbing duration (Non-naturalistic videos) | .255 | 9 | .095 | .852 | 9 | .079 |
| Climbing duration (Naturalistic sounds) | .256 | 9 | .093 | .857 | 9 | .089 |
| Climbing duration (Naturalistic videos) | .198 | 9 | .200* | .909 | 9 | .308 |
| Playing duration (Baseline) | . | 9 | . | . | 9 | . |
| Playing duration (Non-naturalistic sounds) | . | 9 | . | . | 9 | . |
| Playing duration (Non-naturalistic videos) | .519 | 9 | .000 | .390 | 9 | .000 |
| Playing duration (Naturalistic sounds) | .519 | 9 | .000 | .390 | 9 | .000 |
| Playing duration (Naturalistic videos) | .465 | 9 | .000 | .571 | 9 | .000 |
| Out of sight duration (Baseline) | .216 | 9 | .200* | .929 | 9 | .475 |
| Out of sight duration (Non-naturalistic sounds) | .252 | 9 | .104 | .881 | 9 | .162 |
| Out of sight duration (Non-naturalistic videos) | .286 | 9 | .033 | .865 | 9 | .110 |
| Out of sight duration (Naturalistic sounds) | .140 | 9 | .200* | .978 | 9 | .951 |
| Out of sight duration (Naturalistic videos) | .162 | 9 | .200* | .955 | 9 | .743 |
| Pacing duration (Baseline) | .422 | 9 | .000 | .489 | 9 | .000 |
| Pacing duration (Non-naturalistic sounds) | .397 | 9 | .000 | .551 | 9 | .000 |
| Pacing duration (Non-naturalistic videos) | .494 | 9 | .000 | .413 | 9 | .000 |
| Pacing duration (Naturalistic sounds) | .380 | 9 | .000 | .614 | 9 | .000 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Pacing duration (Naturalistic videos) | .447 | 9 | .000 | .530 | 9 | .000 |
| Chewing wires duration (Baseline) | .285 | 9 | .034 | .666 | 9 | .001 |
| Chewing wires duration (Non-naturalistic sounds) | .519 | 9 | .000 | .390 | 9 | .000 |
| Chewing wires duration (Non-naturalistic videos) | .371 | 9 | .001 | .560 | 9 | .000 |
| Chewing wires duration (Naturalistic sounds) | . | 9 | . | . | 9 | . |
| Chewing wires duration (Naturalistic videos) | .187 | 9 | .200* | .872 | 9 | .129 |
| Bathing duration (Non-naturalistic sounds) | . | 9 | . | . | 9 | . |
| Bathing duration (Non-naturalistic videos) | . | 9 | . | . | 9 | . |
| Bathing duration (Baseline) | .519 | 9 | .000 | .390 | 9 | .000 |
| Bathing duration (Naturalistic sounds) | . | 9 | . | . | 9 | . |
| Bathing duration (Naturalistic videos) | . | 9 | . | . | 9 | . |

*. This is a lower bound of the true significance.

a. Lilliefors Significance Correction

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Chewing wires duration (Naturalistic sounds)-Chewing wires duration (Non-naturalistic sounds) | .444 | .745 | .596 | .551 | 1.000 |
| Chewing wires duration (Naturalistic sounds)-Chewing wires duration (Non-naturalistic videos) | .556 | .745 | .745 | .456 | 1.000 |
| Chewing wires duration (Naturalistic sounds)-Chewing wires duration (Baseline) | 1.333 | .745 | 1.789 | .074 | .736 |
| Chewing wires duration (Naturalistic sounds)-Chewing wires duration (Naturalistic videos) | -1.833 | .745 | -2.460 | .014 | .139 |
| Chewing wires duration (Non-naturalistic sounds)-Chewing wires duration (Non-naturalistic videos) | -.111 | .745 | -.149 | .881 | 1.000 |
| Chewing wires duration (Non-naturalistic sounds)-Chewing wires duration (Baseline) | .889 | .745 | 1.193 | .233 | 1.000 |
| Chewing wires duration (Non-naturalistic sounds)-Chewing wires duration (Naturalistic videos) | -1.389 | .745 | -1.863 | .062 | .624 |
| Chewing wires duration (Non-naturalistic videos)-Chewing wires duration (Baseline) | .778 | .745 | 1.043 | .297 | 1.000 |
| Chewing wires duration (Non-naturalistic videos)-Chewing wires duration (Naturalistic videos) | -1.278 | .745 | -1.714 | .086 | .865 |
| Chewing wires duration (Baseline)-Chewing wires duration (Naturalistic videos) | -.500 | .745 | -.671 | .502 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Drinking duration (Non-naturalistic sounds)-Drinking duration (Non-naturalistic videos) | .000 | .745 | .000 | 1.000 | 1.000 |
| Drinking duration (Non-naturalistic sounds)-Drinking duration (Naturalistic sounds) | .000 | .745 | .000 | 1.000 | 1.000 |
| Drinking duration (Non-naturalistic sounds)-Drinking duration (Baseline) | .444 | .745 | .596 | .551 | 1.000 |
| Drinking duration (Non-naturalistic sounds)-Drinking duration (Naturalistic videos) | -.944 | .745 | -1.267 | .205 | 1.000 |
| Drinking duration (Non-naturalistic videos)-Drinking duration (Naturalistic sounds) | .000 | .745 | .000 | 1.000 | 1.000 |
| Drinking duration (Non-naturalistic videos)-Drinking duration (Baseline) | .444 | .745 | .596 | .551 | 1.000 |
| Drinking duration (Non-naturalistic videos)-Drinking duration (Naturalistic videos) | -.944 | .745 | -1.267 | .205 | 1.000 |
| Drinking duration (Naturalistic sounds)-Drinking duration (Baseline) | .444 | .745 | .596 | .551 | 1.000 |
| Drinking duration (Naturalistic sounds)-Drinking duration (Naturalistic videos) | -.944 | .745 | -1.267 | .205 | 1.000 |
| Drinking duration (Baseline)-Drinking duration (Naturalistic videos) | -.500 | .745 | -.671 | .502 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Object manipulation duration (Naturalistic sounds)-Object manipulation duration (Baseline) | .389 | .745 | .522 | .602 | 1.000 |
| Object manipulation duration (Naturalistic sounds)-Object manipulation duration (Non-naturalistic sounds) | .444 | .745 | .596 | .551 | 1.000 |
| Object manipulation duration (Naturalistic sounds)-Object manipulation duration (Non-naturalistic videos) | 1.222 | .745 | 1.640 | .101 | 1.000 |
| Object manipulation duration (Naturalistic sounds)-Object manipulation duration (Naturalistic videos) | -1.556 | .745 | -2.087 | .037 | .369 |
| Object manipulation duration (Baseline)-Object manipulation duration (Non-naturalistic sounds) | -.056 | .745 | -.075 | .941 | 1.000 |
| Object manipulation duration (Baseline)-Object manipulation duration (Non-naturalistic videos) | -.833 | .745 | -1.118 | .264 | 1.000 |
| Object manipulation duration (Baseline)-Object manipulation duration (Naturalistic videos) | -1.167 | .745 | -1.565 | .118 | 1.000 |
| Object manipulation duration (Non-naturalistic sounds)-Object manipulation duration (Non-naturalistic videos) | -.778 | .745 | -1.043 | .297 | 1.000 |
| Object manipulation duration (Non-naturalistic sounds)-Object manipulation duration (Naturalistic videos) | -1.111 | .745 | -1.491 | .136 | 1.000 |
| Object manipulation duration (Non-naturalistic videos)-Object manipulation duration (Naturalistic videos) | -.333 | .745 | -.447 | .655 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Preening duration (Non-naturalistic sounds)-Preening duration (Non-naturalistic videos) | -.500 | .745 | -.671 | .502 | 1.000 |
| Preening duration (Non-naturalistic sounds)-Preening duration (Baseline) | .722 | .745 | .969 | .333 | 1.000 |
| Preening duration (Non-naturalistic sounds)-Preening duration (Naturalistic sounds) | -1.333 | .745 | -1.789 | .074 | .736 |
| Preening duration (Non-naturalistic sounds)-Preening duration (Naturalistic videos) | -2.167 | .745 | -2.907 | .004 | .037 |
| Preening duration (Non-naturalistic videos)-Preening duration (Baseline) | .222 | .745 | .298 | .766 | 1.000 |
| Preening duration (Non-naturalistic videos)-Preening duration (Naturalistic sounds) | -.833 | .745 | -1.118 | .264 | 1.000 |
| Preening duration (Non-naturalistic videos)-Preening duration (Naturalistic videos) | -1.667 | .745 | -2.236 | .025 | .253 |
| Preening duration (Baseline)-Preening duration (Naturalistic sounds) | -.611 | .745 | -.820 | .412 | 1.000 |
| Preening duration (Baseline)-Preening duration (Naturalistic videos) | -1.444 | .745 | -1.938 | .053 | .526 |
| Preening duration (Naturalistic sounds)-Preening duration (Naturalistic videos) | -.833 | .745 | -1.118 | .264 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

## Appendix 3. Additional statistical test results for Chapter 5

Table 1 –Pairwise comparisons in Experiment 1A (transparent lids).

| (I) choice | (J) choice | Mean Difference (I-J) | Std. Error | Sig.[b] | 95% Confidence Interval for Difference[b] | |
|---|---|---|---|---|---|---|
| | | | | | Lower Bound | Upper Bound |
| 1 | 2 | -.013 | .064 | 1.000 | -.285 | .259 |
| | 3 | -.244 | .079 | .433 | -.581 | .094 |
| | 4 | -.208 | .068 | .464 | -.499 | .083 |
| | 5 | -.397* | .055 | .000 | -.632 | -.163 |
| | 6 | -.410* | .067 | .002 | -.696 | -.125 |
| | 7 | -.513* | .079 | .001 | -.849 | -.177 |
| | 8 | -.628* | .100 | .002 | -1.055 | -.202 |
| | 9 | -.718* | .061 | .000 | -.977 | -.459 |
| | 10 | -.833* | .053 | .000 | -1.061 | -.606 |
| 2 | 1 | .013 | .064 | 1.000 | -.259 | .285 |
| | 3 | -.231 | .083 | .768 | -.586 | .124 |
| | 4 | -.195 | .062 | .386 | -.459 | .070 |
| | 5 | -.385* | .048 | .000 | -.588 | -.182 |
| | 6 | -.397* | .092 | .043 | -.787 | -.008 |
| | 7 | -.500* | .082 | .002 | -.850 | -.150 |
| | 8 | -.615* | .099 | .002 | -1.036 | -.195 |
| | 9 | -.705* | .066 | .000 | -.985 | -.425 |
| | 10 | -.821* | .064 | .000 | -1.093 | -.548 |
| 3 | 1 | .244 | .079 | .433 | -.094 | .581 |
| | 2 | .231 | .083 | .768 | -.124 | .586 |
| | 4 | .036 | .087 | 1.000 | -.333 | .404 |
| | 5 | -.154 | .085 | 1.000 | -.517 | .210 |
| | 6 | -.167 | .082 | 1.000 | -.517 | .184 |
| | 7 | -.269 | .120 | 1.000 | -.781 | .242 |
| | 8 | -.385 | .091 | .054 | -.773 | .004 |
| | 9 | -.474* | .092 | .011 | -.867 | -.082 |
| | 10 | -.590* | .088 | .001 | -.963 | -.216 |
| 4 | 1 | .208 | .068 | .464 | -.083 | .499 |
| | 2 | .195 | .062 | .386 | -.070 | .459 |
| | 3 | -.036 | .087 | 1.000 | -.404 | .333 |
| | 5 | -.190 | .062 | .434 | -.453 | .073 |
| | 6 | -.203 | .106 | 1.000 | -.656 | .251 |
| | 7 | -.305 | .107 | .671 | -.763 | .153 |
| | 8 | -.421 | .120 | .194 | -.931 | .090 |
| | 9 | -.510* | .093 | .007 | -.908 | -.113 |
| | 10 | -.626* | .082 | .000 | -.975 | -.276 |
| 5 | 1 | .397* | .055 | .000 | .163 | .632 |
| | 2 | .385* | .048 | .000 | .182 | .588 |
| | 3 | .154 | .085 | 1.000 | -.210 | .517 |
| | 4 | .190 | .062 | .434 | -.073 | .453 |
| | 6 | -.013 | .085 | 1.000 | -.376 | .351 |
| | 7 | -.115 | .087 | 1.000 | -.487 | .256 |
| | 8 | -.231 | .111 | 1.000 | -.703 | .241 |
| | 9 | -.321* | .072 | .035 | -.626 | -.015 |
| | 10 | -.436* | .064 | .001 | -.709 | -.163 |
| 6 | 1 | .410* | .067 | .002 | .125 | .696 |
| | 2 | .397* | .092 | .043 | .008 | .787 |
| | 3 | .167 | .082 | 1.000 | -.184 | .517 |
| | 4 | .203 | .106 | 1.000 | -.251 | .656 |
| | 5 | .013 | .085 | 1.000 | -.351 | .376 |
| | 7 | -.103 | .081 | 1.000 | -.449 | .243 |
| | 8 | -.218 | .061 | .169 | -.477 | .041 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 9 | -.308* | .049 | .002 | -.518 | -.097 |
| | 10 | -.423* | .049 | .000 | -.630 | -.216 |
| 7 | 1 | .513* | .079 | .001 | .177 | .849 |
| | 2 | .500* | .082 | .002 | .150 | .850 |
| | 3 | .269 | .120 | 1.000 | -.242 | .781 |
| | 4 | .305 | .107 | .671 | -.153 | .763 |
| | 5 | .115 | .087 | 1.000 | -.256 | .487 |
| | 6 | .103 | .081 | 1.000 | -.243 | .449 |
| | 8 | -.115 | .091 | 1.000 | -.504 | .273 |
| | 9 | -.205 | .068 | .501 | -.497 | .086 |
| | 10 | -.321* | .058 | .006 | -.568 | -.073 |
| 8 | 1 | .628* | .100 | .002 | .202 | 1.055 |
| | 2 | .615* | .099 | .002 | .195 | 1.036 |
| | 3 | .385 | .091 | .054 | -.004 | .773 |
| | 4 | .421 | .120 | .194 | -.090 | .931 |
| | 5 | .231 | .111 | 1.000 | -.241 | .703 |
| | 6 | .218 | .061 | .169 | -.041 | .477 |
| | 7 | .115 | .091 | 1.000 | -.273 | .504 |
| | 9 | -.090 | .079 | 1.000 | -.427 | .248 |
| | 10 | -.205 | .068 | .501 | -.497 | .086 |
| 9 | 1 | .718* | .061 | .000 | .459 | .977 |
| | 2 | .705* | .066 | .000 | .425 | .985 |
| | 3 | .474* | .092 | .011 | .082 | .867 |
| | 4 | .510* | .093 | .007 | .113 | .908 |
| | 5 | .321* | .072 | .035 | .015 | .626 |
| | 6 | .308* | .049 | .002 | .097 | .518 |
| | 7 | .205 | .068 | .501 | -.086 | .497 |
| | 8 | .090 | .079 | 1.000 | -.248 | .427 |
| | 10 | -.115 | .044 | .980 | -.302 | .071 |
| 10 | 1 | .833* | .053 | .000 | .606 | 1.061 |
| | 2 | .821* | .064 | .000 | .548 | 1.093 |
| | 3 | .590* | .088 | .001 | .216 | .963 |
| | 4 | .626* | .082 | .000 | .276 | .975 |
| | 5 | .436* | .064 | .001 | .163 | .709 |
| | 6 | .423* | .049 | .000 | .216 | .630 |
| | 7 | .321* | .058 | .006 | .073 | .568 |
| | 8 | .205 | .068 | .501 | -.086 | .497 |
| | 9 | .115 | .044 | .980 | -.071 | .302 |

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table 2 – Pairwise comparisons in Experiment 1B (ANOVA for transparent corks and cellophane) for Choice order.

**Pairwise Comparisons**

Measure: MEASURE_1

| (I) choic | (J) choic | Mean Difference (I-J) | Std. Error | Sig.[b] | 95% Confidence Interval for Difference[b] Lower Bound | Upper Bound |
|---|---|---|---|---|---|---|
| 1 | 2 | -.221* | .036 | .002 | -.372 | -.069 |
| | 3 | -.077 | .049 | 1.000 | -.286 | .132 |
| | 4 | -.268 | .065 | .066 | -.546 | .010 |
| | 5 | -.112 | .037 | .499 | -.270 | .047 |
| | 6 | -.282* | .047 | .003 | -.483 | -.081 |
| | 7 | -.267* | .046 | .004 | -.465 | -.069 |
| | 8 | -.346* | .077 | .034 | -.676 | -.016 |
| | 9 | -.355* | .080 | .038 | -.698 | -.013 |
| | 10 | -.478* | .053 | .000 | -.702 | -.255 |
| 2 | 1 | .221* | .036 | .002 | .069 | .372 |
| | 3 | .144 | .054 | .951 | -.087 | .374 |
| | 4 | -.047 | .078 | 1.000 | -.381 | .286 |
| | 5 | .109 | .039 | .763 | -.059 | .276 |
| | 6 | -.062 | .044 | 1.000 | -.248 | .125 |
| | 7 | -.046 | .064 | 1.000 | -.317 | .225 |
| | 8 | -.126 | .093 | 1.000 | -.520 | .269 |
| | 9 | -.135 | .095 | 1.000 | -.537 | .268 |
| | 10 | -.258 | .077 | .263 | -.586 | .070 |
| 3 | 1 | .077 | .049 | 1.000 | -.132 | .286 |
| | 2 | -.144 | .054 | .951 | -.374 | .087 |
| | 4 | -.191 | .075 | 1.000 | -.511 | .129 |
| | 5 | -.035 | .060 | 1.000 | -.291 | .222 |
| | 6 | -.205 | .052 | .088 | -.427 | .016 |
| | 7 | -.190 | .064 | .550 | -.464 | .084 |
| | 8 | -.269 | .098 | .801 | -.687 | .149 |
| | 9 | -.278 | .091 | .435 | -.664 | .107 |
| | 10 | -.401* | .070 | .004 | -.699 | -.104 |
| 4 | 1 | .268 | .065 | .066 | -.010 | .546 |
| | 2 | .047 | .078 | 1.000 | -.286 | .381 |
| | 3 | .191 | .075 | 1.000 | -.129 | .511 |
| | 5 | .156 | .063 | 1.000 | -.112 | .425 |
| | 6 | -.014 | .080 | 1.000 | -.353 | .325 |
| | 7 | .001 | .047 | 1.000 | -.199 | .201 |
| | 8 | -.078 | .065 | 1.000 | -.357 | .200 |
| | 9 | -.087 | .066 | 1.000 | -.369 | .195 |
| | 10 | -.210* | .049 | .045 | -.417 | -.003 |
| 5 | 1 | .112 | .037 | .499 | -.047 | .270 |
| | 2 | -.109 | .039 | .763 | -.276 | .059 |
| | 3 | .035 | .060 | 1.000 | -.222 | .291 |
| | 4 | -.156 | .063 | 1.000 | -.425 | .112 |
| | 6 | -.171 | .044 | .102 | -.358 | .017 |
| | 7 | -.155 | .048 | .312 | -.358 | .048 |
| | 8 | -.235 | .070 | .254 | -.532 | .063 |
| | 9 | -.244 | .078 | .411 | -.578 | .091 |
| | 10 | -.367* | .059 | .002 | -.619 | -.115 |
| 6 | 1 | .282* | .047 | .003 | .081 | .483 |
| | 2 | .062 | .044 | 1.000 | -.125 | .248 |
| | 3 | .205 | .052 | .088 | -.016 | .427 |
| | 4 | .014 | .080 | 1.000 | -.325 | .353 |
| | 5 | .171 | .044 | .102 | -.017 | .358 |
| | 7 | .015 | .062 | 1.000 | -.248 | .279 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 8 | -.064 | .105 | 1.000 | -.509 | .381 |
| | 9 | -.073 | .099 | 1.000 | -.495 | .348 |
| | 10 | -.196 | .080 | 1.000 | -.538 | .146 |
| 7 | 1 | .267* | .046 | .004 | .069 | .465 |
| | 2 | .046 | .064 | 1.000 | -.225 | .317 |
| | 3 | .190 | .064 | .550 | -.084 | .464 |
| | 4 | -.001 | .047 | 1.000 | -.201 | .199 |
| | 5 | .155 | .048 | .312 | -.048 | .358 |
| | 6 | -.015 | .062 | 1.000 | -.279 | .248 |
| | 8 | -.079 | .070 | 1.000 | -.376 | .217 |
| | 9 | -.088 | .050 | 1.000 | -.303 | .126 |
| | 10 | -.212* | .035 | .003 | -.362 | -.061 |
| 8 | 1 | .346* | .077 | .034 | .016 | .676 |
| | 2 | .126 | .093 | 1.000 | -.269 | .520 |
| | 3 | .269 | .098 | .801 | -.149 | .687 |
| | 4 | .078 | .065 | 1.000 | -.200 | .357 |
| | 5 | .235 | .070 | .254 | -.063 | .532 |
| | 6 | .064 | .105 | 1.000 | -.381 | .509 |
| | 7 | .079 | .070 | 1.000 | -.217 | .376 |
| | 9 | -.009 | .071 | 1.000 | -.311 | .293 |
| | 10 | -.132 | .053 | 1.000 | -.360 | .096 |
| 9 | 1 | .355* | .080 | .038 | .013 | .698 |
| | 2 | .135 | .095 | 1.000 | -.268 | .537 |
| | 3 | .278 | .091 | .435 | -.107 | .664 |
| | 4 | .087 | .066 | 1.000 | -.195 | .369 |
| | 5 | .244 | .078 | .411 | -.091 | .578 |
| | 6 | .073 | .099 | 1.000 | -.348 | .495 |
| | 7 | .088 | .050 | 1.000 | -.126 | .303 |
| | 8 | .009 | .071 | 1.000 | -.293 | .311 |
| | 10 | -.123 | .046 | .888 | -.318 | .072 |
| 10 | 1 | .478* | .053 | .000 | .255 | .702 |
| | 2 | .258 | .077 | .263 | -.070 | .586 |
| | 3 | .401* | .070 | .004 | .104 | .699 |
| | 4 | .210* | .049 | .045 | .003 | .417 |
| | 5 | .367* | .059 | .002 | .115 | .619 |
| | 6 | .196 | .080 | 1.000 | -.146 | .538 |
| | 7 | .212* | .035 | .003 | .061 | .362 |
| | 8 | .132 | .053 | 1.000 | -.096 | .360 |
| | 9 | .123 | .046 | .888 | -.072 | .318 |

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table 3 – Pairwise comparisons for the Friedman test for corks in Experiment 1B

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 3 | -.885 | 1.188 | -.745 | .456 | 1.000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 5 | -1.846 | 1.188 | -1.555 | .120 | 1.000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 4 | -2.692 | 1.188 | -2.267 | .023 | 1.000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 2 | -3.231 | 1.188 | -2.721 | .007 | .293 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 7 | -3.538 | 1.188 | -2.980 | .003 | .130 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 6 | -4.000 | 1.188 | -3.368 | .001 | .034 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 8 | -4.500 | 1.188 | -3.789 | .000 | .007 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 9 | -5.577 | 1.188 | -4.696 | .000 | .000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 10 | -6.423 | 1.188 | -5.409 | .000 | .000 |
| Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 5 | -.962 | 1.188 | -.810 | .418 | 1.000 |
| Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 4 | -1.808 | 1.188 | -1.522 | .128 | 1.000 |
| Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 2 | 2.346 | 1.188 | 1.976 | .048 | 1.000 |
| Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 7 | -2.654 | 1.188 | -2.235 | .025 | 1.000 |
| Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 6 | -3.115 | 1.188 | -2.623 | .009 | .392 |
| Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 8 | -3.615 | 1.188 | -3.044 | .002 | .105 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 9** | -4.692 | 1.188 | -3.951 | .000 | .003 |
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 10** | -5.538 | 1.188 | -4.664 | .000 | .000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 4** | .846 | 1.188 | .713 | .476 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 2** | 1.385 | 1.188 | 1.166 | .244 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 7** | -1.692 | 1.188 | -1.425 | .154 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 6** | -2.154 | 1.188 | -1.814 | .070 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 8** | -2.654 | 1.188 | -2.235 | .025 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 9** | -3.731 | 1.188 | -3.142 | .002 | .076 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 10** | -4.577 | 1.188 | -3.854 | .000 | .005 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 2** | .538 | 1.188 | .453 | .650 | 1.000 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 7** | -.846 | 1.188 | -.713 | .476 | 1.000 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 6** | -1.308 | 1.188 | -1.101 | .271 | 1.000 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 8** | -1.808 | 1.188 | -1.522 | .128 | 1.000 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 9** | -2.885 | 1.188 | -2.429 | .015 | .681 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 10** | -3.731 | 1.188 | -3.142 | .002 | .076 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 10** | -3.731 | 1.188 | -3.142 | .002 | .076 |
| **Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 7** | -.308 | 1.188 | -.259 | .796 | 1.000 |
| **Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 6** | -.769 | 1.188 | -.648 | .517 | 1.000 |
| **Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 8** | -1.269 | 1.188 | -1.069 | .285 | 1.000 |
| **Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 9** | -2.346 | 1.188 | -1.976 | .048 | 1.000 |
| **Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 10** | -3.192 | 1.188 | -2.688 | .007 | .323 |
| **Proportion closed, Cork, Choice 7-Proportion closed, Cork, Choice 6** | .462 | 1.188 | .389 | .698 | 1.000 |
| **Proportion closed, Cork, Choice 7-Proportion closed, Cork, Choice 8** | -.962 | 1.188 | -.810 | .418 | 1.000 |
| **Proportion closed, Cork, Choice 7-Proportion closed, Cork, Choice 9** | -2.038 | 1.188 | -1.717 | .086 | 1.000 |
| **Proportion closed, Cork, Choice 7-Proportion closed, Cork, Choice 10** | -2.885 | 1.188 | -2.429 | .015 | .681 |
| **Proportion closed, Cork, Choice 6-Proportion closed, Cork, Choice 8** | -.500 | 1.188 | -.421 | .674 | 1.000 |
| **Proportion closed, Cork, Choice 6-Proportion closed, Cork, Choice 9** | -1.577 | 1.188 | -1.328 | .184 | 1.000 |
| **Proportion closed, Cork, Choice 6-Proportion closed, Cork, Choice 10** | -2.423 | 1.188 | -2.040 | .041 | 1.000 |
| **Proportion closed, Cork, Choice 8-Proportion closed, Cork, Choice 9** | -1.077 | 1.188 | -.907 | .364 | 1.000 |
| **Proportion closed, Cork, Choice 8-Proportion closed, Cork, Choice 10** | -1.923 | 1.188 | -1.619 | .105 | 1.000 |
| **Proportion closed, Cork, Choice 9-Proportion closed, Cork, Choice 10** | -.846 | 1.188 | -.713 | .476 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 4 – Pairwise comparisons for the Friedman test for membrane in Experiment 1B

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 5 | -.269 | 1.188 | -.227 | .821 | 1.000 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 3 | -.731 | 1.188 | -.615 | .538 | 1.000 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 2 | -1.423 | 1.188 | -1.198 | .231 | 1.000 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 7 | -1.846 | 1.188 | -1.555 | .120 | 1.000 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 9 | -2.038 | 1.188 | -1.717 | .086 | 1.000 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 6 | -2.077 | 1.188 | -1.749 | .080 | 1.000 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 8 | -3.115 | 1.188 | -2.623 | .009 | .392 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 4 | -3.962 | 1.188 | -3.336 | .001 | .038 |
| Proportion closed, Cell, Choice 1-Proportion closed, Cell, Choice 10 | -4.154 | 1.188 | -3.498 | .000 | .021 |
| Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 3 | .462 | 1.188 | .389 | .698 | 1.000 |
| Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 2 | 1.154 | 1.188 | .972 | .331 | 1.000 |
| Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 7 | -1.577 | 1.188 | -1.328 | .184 | 1.000 |
| Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 9 | -1.769 | 1.188 | -1.490 | .136 | 1.000 |
| Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 6 | -1.808 | 1.188 | -1.522 | .128 | 1.000 |
| Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 8 | -2.846 | 1.188 | -2.397 | .017 | .745 |
| Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 4 | 3.692 | 1.188 | 3.109 | .002 | .084 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Cell, Choice 5-Proportion closed, Cell, Choice 10** | -3.885 | 1.188 | -3.271 | .001 | .048 |
| **Proportion closed, Cell, Choice 3-Proportion closed, Cell, Choice 2** | .692 | 1.188 | .583 | .560 | 1.000 |
| **Proportion closed, Cell, Choice 3-Proportion closed, Cell, Choice 7** | -1.115 | 1.188 | -.939 | .348 | 1.000 |
| **Proportion closed, Cell, Choice 3-Proportion closed, Cell, Choice 9** | -1.308 | 1.188 | -1.101 | .271 | 1.000 |
| **Proportion closed, Cell, Choice 3-Proportion closed, Cell, Choice 6** | -1.346 | 1.188 | -1.134 | .257 | 1.000 |
| **Proportion closed, Cell, Choice 3-Proportion closed, Cell, Choice 8** | -2.385 | 1.188 | -2.008 | .045 | 1.000 |
| **Proportion closed, Cell, Choice 3-Proportion closed, Cell, Choice 4** | -3.231 | 1.188 | -2.721 | .007 | .293 |
| **Proportion closed, Cell, Choice 3-Proportion closed, Cell, Choice 10** | -3.423 | 1.188 | -2.882 | .004 | .178 |
| **Proportion closed, Cell, Choice 2-Proportion closed, Cell, Choice 7** | -.423 | 1.188 | -.356 | .722 | 1.000 |
| **Proportion closed, Cell, Choice 2-Proportion closed, Cell, Choice 9** | -.615 | 1.188 | -.518 | .604 | 1.000 |
| **Proportion closed, Cell, Choice 2-Proportion closed, Cell, Choice 6** | -.654 | 1.188 | -.551 | .582 | 1.000 |
| **Proportion closed, Cell, Choice 2-Proportion closed, Cell, Choice 8** | -1.692 | 1.188 | -1.425 | .154 | 1.000 |
| **Proportion closed, Cell, Choice 2-Proportion closed, Cell, Choice 4** | -2.538 | 1.188 | -2.138 | .033 | 1.000 |
| **Proportion closed, Cell, Choice 2-Proportion closed, Cell, Choice 10** | -2.731 | 1.188 | -2.300 | .021 | .966 |
| **Proportion closed, Cell, Choice 7-Proportion closed, Cell, Choice 9** | -.192 | 1.188 | -.162 | .871 | 1.000 |
| **Proportion closed, Cell, Choice 7-Proportion closed, Cell, Choice 6** | .231 | 1.188 | .194 | .846 | 1.000 |
| **Proportion closed, Cell, Choice 7-Proportion closed, Cell, Choice 8** | -1.269 | 1.188 | -1.069 | .285 | 1.000 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Cell, Choice 7-Proportion closed, Cell, Choice 8** | -1.269 | 1.188 | -1.069 | .285 | 1.000 |
| **Proportion closed, Cell, Choice 7-Proportion closed, Cell, Choice 4** | 2.115 | 1.188 | 1.781 | .075 | 1.000 |
| **Proportion closed, Cell, Choice 7-Proportion closed, Cell, Choice 10** | -2.308 | 1.188 | -1.943 | .052 | 1.000 |
| **Proportion closed, Cell, Choice 9-Proportion closed, Cell, Choice 6** | .038 | 1.188 | .032 | .974 | 1.000 |
| **Proportion closed, Cell, Choice 9-Proportion closed, Cell, Choice 8** | 1.077 | 1.188 | .907 | .364 | 1.000 |
| **Proportion closed, Cell, Choice 9-Proportion closed, Cell, Choice 4** | 1.923 | 1.188 | 1.619 | .105 | 1.000 |
| **Proportion closed, Cell, Choice 9-Proportion closed, Cell, Choice 10** | -2.115 | 1.188 | -1.781 | .075 | 1.000 |
| **Proportion closed, Cell, Choice 6-Proportion closed, Cell, Choice 8** | -1.038 | 1.188 | -.874 | .382 | 1.000 |
| **Proportion closed, Cell, Choice 6-Proportion closed, Cell, Choice 4** | 1.885 | 1.188 | 1.587 | .113 | 1.000 |
| **Proportion closed, Cell, Choice 6-Proportion closed, Cell, Choice 10** | -2.077 | 1.188 | -1.749 | .080 | 1.000 |
| **Proportion closed, Cell, Choice 8-Proportion closed, Cell, Choice 4** | .846 | 1.188 | .713 | .476 | 1.000 |
| **Proportion closed, Cell, Choice 8-Proportion closed, Cell, Choice 10** | -1.038 | 1.188 | -.874 | .382 | 1.000 |
| **Proportion closed, Cell, Choice 4-Proportion closed, Cell, Choice 10** | -.192 | 1.188 | -.162 | .871 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 5 – Pairwise comparisons in Experiment 1C (opaque lids) for Choice order.

**Pairwise Comparisons**

Measure: prop

| (I) choice | (J) choice | Mean Difference (I-J) | Std. Error | Sig.[b] | 95% Confidence Interval for Difference[b] | |
|---|---|---|---|---|---|---|
| | | | | | Lower Bound | Upper Bound |
| 1 | 2 | -.042 | .030 | 1.000 | -.172 | .089 |
| | 3 | -.014 | .014 | 1.000 | -.075 | .047 |
| | 4 | -.139 | .050 | .773 | -.356 | .078 |
| | 5 | -.283* | .060 | .028 | -.546 | -.021 |
| | 6 | -.806* | .050 | .000 | -1.022 | -.589 |
| | 7 | -.847* | .066 | .000 | -1.137 | -.557 |
| | 8 | -.917* | .048 | .000 | -1.127 | -.706 |
| | 9 | -.928* | .033 | .000 | -1.072 | -.783 |
| | 10 | -.979* | .021 | .000 | -1.070 | -.888 |
| 2 | 1 | .042 | .030 | 1.000 | -.089 | .172 |
| | 3 | .028 | .019 | 1.000 | -.054 | .110 |
| | 4 | -.097 | .052 | 1.000 | -.325 | .131 |
| | 5 | -.242* | .053 | .039 | -.475 | -.008 |
| | 6 | -.764* | .066 | .000 | -1.054 | -.474 |
| | 7 | -.806* | .091 | .000 | -1.205 | -.406 |
| | 8 | -.875* | .065 | .000 | -1.160 | -.590 |
| | 9 | -.886* | .038 | .000 | -1.052 | -.720 |
| | 10 | -.938* | .034 | .000 | -1.087 | -.788 |
| 3 | 1 | .014 | .014 | 1.000 | -.047 | .075 |
| | 2 | -.028 | .019 | 1.000 | -.110 | .054 |
| | 4 | -.125 | .046 | .944 | -.328 | .078 |
| | 5 | -.269* | .053 | .016 | -.502 | -.037 |
| | 6 | -.792* | .055 | .000 | -1.031 | -.552 |
| | 7 | -.833* | .079 | .000 | -1.181 | -.486 |
| | 8 | -.903* | .056 | .000 | -1.148 | -.658 |
| | 9 | -.914* | .033 | .000 | -1.059 | -.769 |
| | 10 | -.965* | .024 | .000 | -1.070 | -.860 |
| 4 | 1 | .139 | .050 | .773 | -.078 | .356 |
| | 2 | .097 | .052 | 1.000 | -.131 | .325 |
| | 3 | .125 | .046 | .944 | -.078 | .328 |
| | 5 | -.144 | .058 | 1.000 | -.398 | .109 |
| | 6 | -.667* | .087 | .000 | -1.047 | -.286 |
| | 7 | -.708* | .096 | .001 | -1.130 | -.286 |
| | 8 | -.778* | .093 | .000 | -1.182 | -.373 |
| | 9 | -.789* | .055 | .000 | -1.028 | -.550 |
| | 10 | -.840* | .049 | .000 | -1.053 | -.628 |
| 5 | 1 | .283* | .060 | .028 | .021 | .546 |
| | 2 | .242* | .053 | .039 | .008 | .475 |
| | 3 | .269* | .053 | .016 | .037 | .502 |
| | 4 | .144 | .058 | 1.000 | -.109 | .398 |
| | 6 | -.522* | .097 | .010 | -.947 | -.098 |
| | 7 | -.564* | .112 | .017 | -1.053 | -.075 |
| | 8 | -.633* | .098 | .002 | -1.062 | -.205 |
| | 9 | -.644* | .070 | .000 | -.951 | -.338 |
| | 10 | -.696* | .054 | .000 | -.934 | -.458 |
| 6 | 1 | .806* | .050 | .000 | .589 | 1.022 |
| | 2 | .764* | .066 | .000 | .474 | 1.054 |
| | 3 | .792* | .055 | .000 | .552 | 1.031 |
| | 4 | .667* | .087 | .000 | .286 | 1.047 |
| | 5 | .522* | .097 | .010 | .098 | .947 |
| | 7 | -.042 | .080 | 1.000 | -.391 | .307 |
| | 8 | -.111 | .043 | 1.000 | -.298 | .076 |
| | 9 | -.122 | .070 | 1.000 | -.426 | .182 |
| | 10 | -.174 | .060 | .670 | -.437 | .090 |
| 7 | 1 | .847* | .066 | .000 | .557 | 1.137 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 2 | .806* | .091 | .000 | .406 | 1.205 |
| | 3 | .833* | .079 | .000 | .486 | 1.181 |
| | 4 | .708* | .096 | .001 | .286 | 1.130 |
| | 5 | .564* | .112 | .017 | .075 | 1.053 |
| | 6 | .042 | .080 | 1.000 | -.307 | .391 |
| | 8 | -.069 | .066 | 1.000 | -.360 | .221 |
| | 9 | -.081 | .076 | 1.000 | -.414 | .253 |
| | 10 | -.132 | .074 | 1.000 | -.454 | .190 |
| 8 | 1 | .917* | .048 | .000 | .706 | 1.127 |
| | 2 | .875* | .065 | .000 | .590 | 1.160 |
| | 3 | .903* | .056 | .000 | .658 | 1.148 |
| | 4 | .778* | .093 | .000 | .373 | 1.182 |
| | 5 | .633* | .098 | .002 | .205 | 1.062 |
| | 6 | .111 | .043 | 1.000 | -.076 | .298 |
| | 7 | .069 | .066 | 1.000 | -.221 | .360 |
| | 9 | -.011 | .067 | 1.000 | -.305 | .282 |
| | 10 | -.063 | .055 | 1.000 | -.305 | .180 |
| 9 | 1 | .928* | .033 | .000 | .783 | 1.072 |
| | 2 | .886* | .038 | .000 | .720 | 1.052 |
| | 3 | .914* | .033 | .000 | .769 | 1.059 |
| | 4 | .789* | .055 | .000 | .550 | 1.028 |
| | 5 | .644* | .070 | .000 | .338 | .951 |
| | 6 | .122 | .070 | 1.000 | -.182 | .426 |
| | 7 | .081 | .076 | 1.000 | -.253 | .414 |
| | 8 | .011 | .067 | 1.000 | -.282 | .305 |
| | 10 | -.051 | .032 | 1.000 | -.193 | .090 |
| 10 | 1 | .979* | .021 | .000 | .888 | 1.070 |
| | 2 | .938* | .034 | .000 | .788 | 1.087 |
| | 3 | .965* | .024 | .000 | .860 | 1.070 |
| | 4 | .840* | .049 | .000 | .628 | 1.053 |
| | 5 | .696* | .054 | .000 | .458 | .934 |
| | 6 | .174 | .060 | .670 | -.090 | .437 |
| | 7 | .132 | .074 | 1.000 | -.190 | .454 |
| | 8 | .063 | .055 | 1.000 | -.180 | .305 |
| | 9 | .051 | .032 | 1.000 | -.090 | .193 |

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table 6 – Two-way, repeated measures ANOVA pairwise comparisons in Experiment 1C (opaque corks and paper) for Choice order.

**Pairwise Comparisons**

Measure: prop

| (I) f2 | (J) f2 | Mean Difference (I-J) | Std. Error | Sig.[b] | 95% Confidence Interval for Difference[b] Lower Bound | Upper Bound |
|---|---|---|---|---|---|---|
| 1 | 2 | -.138 | .059 | 1.000 | -.403 | .128 |
| | 3 | -.182 | .051 | .228 | -.412 | .048 |
| | 4 | -.242 | .059 | .094 | -.508 | .024 |
| | 5 | -.342* | .064 | .015 | -.633 | -.052 |
| | 6 | -.600* | .056 | .000 | -.853 | -.347 |
| | 7 | -.705* | .085 | .000 | -1.089 | -.320 |
| | 8 | -.848* | .060 | .000 | -1.121 | -.576 |
| | 9 | -.839* | .042 | .000 | -1.031 | -.647 |
| | 10 | -.874* | .044 | .000 | -1.073 | -.675 |
| 2 | 1 | .138 | .059 | 1.000 | -.128 | .403 |
| | 3 | -.044 | .074 | 1.000 | -.376 | .289 |
| | 4 | -.105 | .039 | 1.000 | -.282 | .073 |
| | 5 | -.205 | .095 | 1.000 | -.635 | .226 |
| | 6 | -.462* | .102 | .047 | -.921 | -.003 |
| | 7 | -.567 | .137 | .091 | -1.186 | .053 |
| | 8 | -.711* | .082 | .000 | -1.081 | -.341 |
| | 9 | -.702* | .080 | .000 | -1.061 | -.342 |
| | 10 | -.736* | .071 | .000 | -1.055 | -.417 |
| 3 | 1 | .182 | .051 | .228 | -.048 | .412 |
| | 2 | .044 | .074 | 1.000 | -.289 | .376 |
| | 4 | -.061 | .056 | 1.000 | -.315 | .194 |
| | 5 | -.161 | .081 | 1.000 | -.527 | .206 |
| | 6 | -.418* | .057 | .001 | -.677 | -.160 |
| | 7 | -.523* | .099 | .016 | -.969 | -.077 |
| | 8 | -.667* | .069 | .000 | -.977 | -.357 |
| | 9 | -.658* | .069 | .000 | -.967 | -.348 |
| | 10 | -.692* | .063 | .000 | -.978 | -.407 |
| 4 | 1 | .242 | .059 | .094 | -.024 | .508 |
| | 2 | .105 | .039 | 1.000 | -.073 | .282 |
| | 3 | .061 | .056 | 1.000 | -.194 | .315 |
| | 5 | -.100 | .078 | 1.000 | -.454 | .254 |
| | 6 | -.358 | .090 | .120 | -.765 | .050 |
| | 7 | -.462 | .133 | .265 | -1.061 | .137 |
| | 8 | -.606* | .083 | .001 | -.983 | -.229 |
| | 9 | -.597* | .084 | .001 | -.976 | -.218 |
| | 10 | -.632* | .073 | .000 | -.961 | -.302 |
| 5 | 1 | .342* | .064 | .015 | .052 | .633 |
| | 2 | .205 | .095 | 1.000 | -.226 | .635 |
| | 3 | .161 | .081 | 1.000 | -.206 | .527 |
| | 4 | .100 | .078 | 1.000 | -.254 | .454 |
| | 6 | -.258 | .076 | .317 | -.602 | .087 |
| | 7 | -.362 | .107 | .306 | -.844 | .119 |
| | 8 | -.506* | .101 | .024 | -.963 | -.049 |
| | 9 | -.497* | .089 | .011 | -.899 | -.095 |
| | 10 | -.532* | .092 | .008 | -.947 | -.117 |
| 6 | 1 | .600* | .056 | .000 | .347 | .853 |
| | 2 | .462* | .102 | .047 | .003 | .921 |
| | 3 | .418* | .057 | .001 | .160 | .677 |
| | 4 | .358 | .090 | .120 | -.050 | .765 |
| | 5 | .258 | .076 | .317 | -.087 | .602 |
| | 7 | -.105 | .054 | 1.000 | -.350 | .141 |
| | 8 | -.248 | .056 | .055 | -.500 | .003 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 9 | -.239* | .052 | .041 | -.472 | -.006 |
| | 10 | -.274* | .058 | .034 | -.534 | -.014 |
| 7 | 1 | .705* | .085 | .000 | .320 | 1.089 |
| | 2 | .567 | .137 | .091 | -.053 | 1.186 |
| | 3 | .523* | .099 | .016 | .077 | .969 |
| | 4 | .462 | .133 | .265 | -.137 | 1.061 |
| | 5 | .362 | .107 | .306 | -.119 | .844 |
| | 6 | .105 | .054 | 1.000 | -.141 | .350 |
| | 8 | -.144 | .075 | 1.000 | -.481 | .193 |
| | 9 | -.135 | .067 | 1.000 | -.436 | .166 |
| | 10 | -.170 | .078 | 1.000 | -.523 | .183 |
| 8 | 1 | .848* | .060 | .000 | .576 | 1.121 |
| | 2 | .711* | .082 | .000 | .341 | 1.081 |
| | 3 | .667* | .069 | .000 | .357 | .977 |
| | 4 | .606* | .083 | .001 | .229 | .983 |
| | 5 | .506* | .101 | .024 | .049 | .963 |
| | 6 | .248 | .056 | .055 | -.003 | .500 |
| | 7 | .144 | .075 | 1.000 | -.193 | .481 |
| | 9 | .009 | .033 | 1.000 | -.140 | .158 |
| | 10 | -.026 | .029 | 1.000 | -.156 | .104 |
| 9 | 1 | .839* | .042 | .000 | .647 | 1.031 |
| | 2 | .702* | .080 | .000 | .342 | 1.061 |
| | 3 | .658* | .069 | .000 | .348 | .967 |
| | 4 | .597* | .084 | .001 | .218 | .976 |
| | 5 | .497* | .089 | .011 | .095 | .899 |
| | 6 | .239* | .052 | .041 | .006 | .472 |
| | 7 | .135 | .067 | 1.000 | -.166 | .436 |
| | 8 | -.009 | .033 | 1.000 | -.158 | .140 |
| | 10 | -.035 | .024 | 1.000 | -.144 | .075 |
| 10 | 1 | .874* | .044 | .000 | .675 | 1.073 |
| | 2 | .736* | .071 | .000 | .417 | 1.055 |
| | 3 | .692* | .063 | .000 | .407 | .978 |
| | 4 | .632* | .073 | .000 | .302 | .961 |
| | 5 | .532* | .092 | .008 | .117 | .947 |
| | 6 | .274* | .058 | .034 | .014 | .534 |
| | 7 | .170 | .078 | 1.000 | -.183 | .523 |
| | 8 | .026 | .029 | 1.000 | -.104 | .156 |
| | 9 | .035 | .024 | 1.000 | -.075 | .144 |

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table 7 – Friedman test pairwise comparisons in Experiment 1C (opaque corks) for Choice order.

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 2 | -.682 | 1.291 | -.528 | .597 | 1.000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 3 | -1.818 | 1.291 | -1.408 | .159 | 1.000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 4 | -2.136 | 1.291 | -1.655 | .098 | 1.000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 5 | -3.455 | 1.291 | -2.676 | .007 | .335 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 6 | -4.182 | 1.291 | -3.239 | .001 | .054 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 7 | -4.864 | 1.291 | -3.767 | .000 | .007 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 9 | -5.909 | 1.291 | -4.577 | .000 | .000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 10 | -6.091 | 1.291 | -4.718 | .000 | .000 |
| Proportion closed, Cork, Choice 1-Proportion closed, Cork, Choice 8 | -6.773 | 1.291 | -5.246 | .000 | .000 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 3 | -1.136 | 1.291 | -.880 | .379 | 1.000 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 4 | -1.455 | 1.291 | -1.127 | .260 | 1.000 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 5 | -2.773 | 1.291 | -2.148 | .032 | 1.000 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 6 | -3.500 | 1.291 | -2.711 | .007 | .302 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 7 | -4.182 | 1.291 | -3.239 | .001 | .054 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 9 | -5.227 | 1.291 | -4.049 | .000 | .002 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 10 | -5.409 | 1.291 | -4.190 | .000 | .001 |
| Proportion closed, Cork, Choice 2-Proportion closed, Cork, Choice 8 | -6.091 | 1.291 | -4.718 | .000 | .000 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 4** | -.318 | 1.291 | -.246 | .805 | 1.000 |
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 5** | -1.636 | 1.291 | -1.268 | .205 | 1.000 |
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 6** | -2.364 | 1.291 | -1.831 | .067 | 1.000 |
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 7** | -3.045 | 1.291 | -2.359 | .018 | .825 |
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 9** | -4.091 | 1.291 | -3.169 | .002 | .069 |
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 10** | -4.273 | 1.291 | -3.310 | .001 | .042 |
| **Proportion closed, Cork, Choice 3-Proportion closed, Cork, Choice 8** | -4.955 | 1.291 | -3.838 | .000 | .006 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 5** | -1.318 | 1.291 | -1.021 | .307 | 1.000 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 6** | -2.045 | 1.291 | -1.584 | .113 | 1.000 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 7** | -2.727 | 1.291 | -2.113 | .035 | 1.000 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 9** | -3.773 | 1.291 | -2.922 | .003 | .156 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 10** | -3.955 | 1.291 | -3.063 | .002 | .099 |
| **Proportion closed, Cork, Choice 4-Proportion closed, Cork, Choice 8** | -4.636 | 1.291 | -3.591 | .000 | .015 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 6** | -.727 | 1.291 | -.563 | .573 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 7** | -1.409 | 1.291 | -1.091 | .275 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 9** | -2.455 | 1.291 | -1.901 | .057 | 1.000 |
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 10** | -2.636 | 1.291 | -2.042 | .041 | 1.000 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Cork, Choice 5-Proportion closed, Cork, Choice 8** | -3.318 | 1.291 | -2.570 | .010 | .457 |
| **Proportion closed, Cork, Choice 6-Proportion closed, Cork, Choice 7** | -.682 | 1.291 | -.528 | .597 | 1.000 |
| **Proportion closed, Cork, Choice 6-Proportion closed, Cork, Choice 9** | -1.727 | 1.291 | -1.338 | .181 | 1.000 |
| **Proportion closed, Cork, Choice 6-Proportion closed, Cork, Choice 10** | -1.909 | 1.291 | -1.479 | .139 | 1.000 |
| **Proportion closed, Cork, Choice 6-Proportion closed, Cork, Choice 8** | -2.591 | 1.291 | -2.007 | .045 | 1.000 |
| **Proportion closed, Cork, Choice 7-Proportion closed, Cork, Choice 9** | -1.045 | 1.291 | -.810 | .418 | 1.000 |
| **Proportion closed, Cork, Choice 7-Proportion closed, Cork, Choice 10** | -1.227 | 1.291 | -.951 | .342 | 1.000 |
| **Proportion closed, Cork, Choice 7-Proportion closed, Cork, Choice 8** | -1.909 | 1.291 | -1.479 | .139 | 1.000 |
| **Proportion closed, Cork, Choice 9-Proportion closed, Cork, Choice 10** | -.182 | 1.291 | -.141 | .888 | 1.000 |
| **Proportion closed, Cork, Choice 9-Proportion closed, Cork, Choice 8** | .864 | 1.291 | .669 | .504 | 1.000 |
| **Proportion closed, Cork, Choice 10-Proportion closed, Cork, Choice 8** | .682 | 1.291 | .528 | .597 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 8 – Friedman test pairwise comparisons in Experiment 1C (opaque membrane) for Choice order.

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 2 | -1.125 | 1.236 | -.910 | .363 | 1.000 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 3 | -1.333 | 1.236 | -1.079 | .281 | 1.000 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 4 | -1.500 | 1.236 | -1.214 | .225 | 1.000 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 5 | -2.292 | 1.236 | -1.854 | .064 | 1.000 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 6 | -4.792 | 1.236 | -3.877 | .000 | .005 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 7 | -5.125 | 1.236 | -4.146 | .000 | .002 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 8 | -5.917 | 1.236 | -4.787 | .000 | .000 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 9 | -6.250 | 1.236 | -5.056 | .000 | .000 |
| Proportion closed, Paper, Choice 1-Proportion closed, Paper, Choice 10 | -6.667 | 1.236 | -5.394 | .000 | .000 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 3 | -.208 | 1.236 | -.169 | .866 | 1.000 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 4 | -.375 | 1.236 | -.303 | .762 | 1.000 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 5 | -1.167 | 1.236 | -.944 | .345 | 1.000 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 6 | -3.667 | 1.236 | -2.966 | .003 | .136 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 7 | -4.000 | 1.236 | -3.236 | .001 | .055 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 8 | -4.792 | 1.236 | -3.877 | .000 | .005 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 9 | -5.125 | 1.236 | -4.146 | .000 | .002 |
| Proportion closed, Paper, Choice 2-Proportion closed, Paper, Choice 10 | -5.542 | 1.236 | -4.483 | .000 | .000 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Paper, Choice 3-Proportion closed, Paper, Choice 4** | -.167 | 1.236 | -.135 | .893 | 1.000 |
| **Proportion closed, Paper, Choice 3-Proportion closed, Paper, Choice 5** | -.958 | 1.236 | -.775 | .438 | 1.000 |
| **Proportion closed, Paper, Choice 3-Proportion closed, Paper, Choice 6** | -3.458 | 1.236 | -2.798 | .005 | .231 |
| **Proportion closed, Paper, Choice 3-Proportion closed, Paper, Choice 7** | -3.792 | 1.236 | -3.068 | .002 | .097 |
| **Proportion closed, Paper, Choice 3-Proportion closed, Paper, Choice 8** | -4.583 | 1.236 | -3.708 | .000 | .009 |
| **Proportion closed, Paper, Choice 3-Proportion closed, Paper, Choice 9** | -4.917 | 1.236 | -3.978 | .000 | .003 |
| **Proportion closed, Paper, Choice 3-Proportion closed, Paper, Choice 10** | -5.333 | 1.236 | -4.315 | .000 | .001 |
| **Proportion closed, Paper, Choice 4-Proportion closed, Paper, Choice 5** | -.792 | 1.236 | -.640 | .522 | 1.000 |
| **Proportion closed, Paper, Choice 4-Proportion closed, Paper, Choice 6** | -3.292 | 1.236 | -2.663 | .008 | .348 |
| **Proportion closed, Paper, Choice 4-Proportion closed, Paper, Choice 7** | -3.625 | 1.236 | -2.933 | .003 | .151 |
| **Proportion closed, Paper, Choice 4-Proportion closed, Paper, Choice 8** | -4.417 | 1.236 | -3.573 | .000 | .016 |
| **Proportion closed, Paper, Choice 4-Proportion closed, Paper, Choice 9** | -4.750 | 1.236 | -3.843 | .000 | .005 |
| **Proportion closed, Paper, Choice 4-Proportion closed, Paper, Choice 10** | -5.167 | 1.236 | -4.180 | .000 | .001 |
| **Proportion closed, Paper, Choice 5-Proportion closed, Paper, Choice 6** | -2.500 | 1.236 | -2.023 | .043 | 1.000 |
| **Proportion closed, Paper, Choice 5-Proportion closed, Paper, Choice 7** | -2.833 | 1.236 | -2.292 | .022 | .985 |
| **Proportion closed, Paper, Choice 5-Proportion closed, Paper, Choice 8** | -3.625 | 1.236 | -2.933 | .003 | .151 |
| **Proportion closed, Paper, Choice 5-Proportion closed, Paper, Choice 9** | -3.958 | 1.236 | -3.202 | .001 | .061 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion closed, Paper, Choice 5-Proportion closed, Paper, Choice 10** | -4.375 | 1.236 | -3.540 | .000 | .018 |
| **Proportion closed, Paper, Choice 6-Proportion closed, Paper, Choice 7** | -.333 | 1.236 | -.270 | .787 | 1.000 |
| **Proportion closed, Paper, Choice 6-Proportion closed, Paper, Choice 8** | -1.125 | 1.236 | -.910 | .363 | 1.000 |
| **Proportion closed, Paper, Choice 6-Proportion closed, Paper, Choice 9** | -1.458 | 1.236 | -1.180 | .238 | 1.000 |
| **Proportion closed, Paper, Choice 6-Proportion closed, Paper, Choice 10** | -1.875 | 1.236 | -1.517 | .129 | 1.000 |
| **Proportion closed, Paper, Choice 7-Proportion closed, Paper, Choice 8** | -.792 | 1.236 | -.640 | .522 | 1.000 |
| **Proportion closed, Paper, Choice 7-Proportion closed, Paper, Choice 9** | -1.125 | 1.236 | -.910 | .363 | 1.000 |
| **Proportion closed, Paper, Choice 7-Proportion closed, Paper, Choice 10** | -1.542 | 1.236 | -1.247 | .212 | 1.000 |
| **Proportion closed, Paper, Choice 8-Proportion closed, Paper, Choice 9** | -.333 | 1.236 | -.270 | .787 | 1.000 |
| **Proportion closed, Paper, Choice 8-Proportion closed, Paper, Choice 10** | -.750 | 1.236 | -.607 | .544 | 1.000 |
| **Proportion closed, Paper, Choice 9-Proportion closed, Paper, Choice 10** | -.417 | 1.236 | -.337 | .736 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 10 – Pairwise comparisons in Experiment 2 (opaque versus transparent manipulanda) for type of manipulandum.

**Pairwise Comparisons**

Measure: MEASURE_1

| (I) manip | (J) manip | Mean Difference (I-J) | Std. Error | Sig.[a] | 95% Confidence Interval for Difference[a] | |
|---|---|---|---|---|---|---|
| | | | | | Lower Bound | Upper Bound |
| 1 | 2 | -.010 | .004 | .121 | -.023 | .002 |
| | 3 | .002 | .003 | 1.000 | -.007 | .010 |
| 2 | 1 | .010 | .004 | .121 | -.002 | .023 |
| | 3 | .012 | .005 | .158 | -.004 | .028 |
| 3 | 1 | -.002 | .003 | 1.000 | -.010 | .007 |
| | 2 | -.012 | .005 | .158 | -.028 | .004 |

Based on estimated marginal means

a. Adjustment for multiple comparisons: Bonferroni.

Table 11 – Pairwise comparisons for the two-way repeated measures ANOVA in Experiment 2 (opaque versus transparent manipulanda) and choice order.

**Pairwise Comparisons**

Measure: MEASURE_1

| (I) choice | (J) choice | Mean Difference (I-J) | Std. Error | Sig.[b] | 95% Confidence Interval for Difference[b] | |
|---|---|---|---|---|---|---|
| | | | | | Lower Bound | Upper Bound |
| 1 | 2 | -.001 | .048 | 1.000 | -.225 | .223 |
| | 3 | -.034 | .059 | 1.000 | -.311 | .242 |
| | 4 | -.022 | .065 | 1.000 | -.327 | .283 |
| | 5 | -.127 | .062 | 1.000 | -.420 | .167 |
| | 6 | -.170 | .067 | 1.000 | -.487 | .147 |
| | 7 | -.229 | .074 | .561 | -.575 | .117 |
| | 8 | -.228 | .072 | .532 | -.569 | .113 |
| | 9 | -.338* | .067 | .033 | -.656 | -.021 |
| | 10 | -.357 | .082 | .082 | -.742 | .028 |
| 2 | 1 | .001 | .048 | 1.000 | -.223 | .225 |
| | 3 | -.033 | .068 | 1.000 | -.351 | .285 |
| | 4 | -.021 | .049 | 1.000 | -.250 | .208 |
| | 5 | -.126 | .031 | .131 | -.272 | .020 |
| | 6 | -.169 | .064 | 1.000 | -.471 | .133 |
| | 7 | -.228 | .057 | .144 | -.497 | .041 |
| | 8 | -.227 | .055 | .121 | -.487 | .034 |
| | 9 | -.337* | .056 | .009 | -.600 | -.075 |
| | 10 | -.356* | .068 | .024 | -.674 | -.037 |
| 3 | 1 | .034 | .059 | 1.000 | -.242 | .311 |
| | 2 | .033 | .068 | 1.000 | -.285 | .351 |
| | 4 | .012 | .060 | 1.000 | -.271 | .296 |
| | 5 | -.092 | .080 | 1.000 | -.468 | .284 |
| | 6 | -.136 | .062 | 1.000 | -.425 | .154 |
| | 7 | -.194 | .067 | .777 | -.509 | .120 |
| | 8 | -.193 | .068 | .868 | -.513 | .127 |
| | 9 | -.304 | .072 | .097 | -.641 | .033 |
| | 10 | -.322 | .087 | .216 | -.730 | .086 |
| 4 | 1 | .022 | .065 | 1.000 | -.283 | .327 |
| | 2 | .021 | .049 | 1.000 | -.208 | .250 |
| | 3 | -.012 | .060 | 1.000 | -.296 | .271 |
| | 5 | -.104 | .054 | 1.000 | -.358 | .149 |
| | 6 | -.148 | .066 | 1.000 | -.458 | .162 |
| | 7 | -.207 | .066 | .550 | -.518 | .105 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 8 | -.206 | .056 | .233 | -.469 | .058 |
| | 9 | -.316* | .044 | .002 | -.524 | -.109 |
| | 10 | -.334* | .055 | .008 | -.593 | -.076 |
| 5 | 1 | .127 | .062 | 1.000 | -.167 | .420 |
| | 2 | .126 | .031 | .131 | -.020 | .272 |
| | 3 | .092 | .080 | 1.000 | -.284 | .468 |
| | 4 | .104 | .054 | 1.000 | -.149 | .358 |
| | 6 | -.043 | .067 | 1.000 | -.360 | .274 |
| | 7 | -.102 | .070 | 1.000 | -.433 | .229 |
| | 8 | -.101 | .050 | 1.000 | -.335 | .133 |
| | 9 | -.212 | .061 | .315 | -.498 | .075 |
| | 10 | -.230 | .054 | .100 | -.486 | .026 |
| 6 | 1 | .170 | .067 | 1.000 | -.147 | .487 |
| | 2 | .169 | .064 | 1.000 | -.133 | .471 |
| | 3 | .136 | .062 | 1.000 | -.154 | .425 |
| | 4 | .148 | .066 | 1.000 | -.162 | .458 |
| | 5 | .043 | .067 | 1.000 | -.274 | .360 |
| | 7 | -.059 | .040 | 1.000 | -.246 | .129 |
| | 8 | -.058 | .053 | 1.000 | -.306 | .191 |
| | 9 | -.168 | .050 | .357 | -.402 | .065 |
| | 10 | -.187 | .057 | .452 | -.457 | .084 |
| 7 | 1 | .229 | .074 | .561 | -.117 | .575 |
| | 2 | .228 | .057 | .144 | -.041 | .497 |
| | 3 | .194 | .067 | .777 | -.120 | .509 |
| | 4 | .207 | .066 | .550 | -.105 | .518 |
| | 5 | .102 | .070 | 1.000 | -.229 | .433 |
| | 6 | .059 | .040 | 1.000 | -.129 | .246 |
| | 8 | .001 | .054 | 1.000 | -.252 | .254 |
| | 9 | -.109 | .046 | 1.000 | -.324 | .105 |
| | 10 | -.128 | .070 | 1.000 | -.455 | .200 |
| 8 | 1 | .228 | .072 | .532 | -.113 | .569 |
| | 2 | .227 | .055 | .121 | -.034 | .487 |
| | 3 | .193 | .068 | .868 | -.127 | .513 |
| | 4 | .206 | .056 | .233 | -.058 | .469 |
| | 5 | .101 | .050 | 1.000 | -.133 | .335 |
| | 6 | .058 | .053 | 1.000 | -.191 | .306 |
| | 7 | -.001 | .054 | 1.000 | -.254 | .252 |
| | 9 | -.111 | .038 | .776 | -.289 | .068 |
| | 10 | -.129 | .037 | .325 | -.304 | .047 |
| 9 | 1 | .338* | .067 | .033 | .021 | .656 |
| | 2 | .337* | .056 | .009 | .075 | .600 |
| | 3 | .304 | .072 | .097 | -.033 | .641 |
| | 4 | .316* | .044 | .002 | .109 | .524 |
| | 5 | .212 | .061 | .315 | -.075 | .498 |
| | 6 | .168 | .050 | .357 | -.065 | .402 |
| | 7 | .109 | .046 | 1.000 | -.105 | .324 |
| | 8 | .111 | .038 | .776 | -.068 | .289 |
| | 10 | -.018 | .037 | 1.000 | -.192 | .156 |
| 10 | 1 | .357 | .082 | .082 | -.028 | .742 |
| | 2 | .356* | .068 | .024 | .037 | .674 |
| | 3 | .322 | .087 | .216 | -.086 | .730 |
| | 4 | .334* | .055 | .008 | .076 | .593 |
| | 5 | .230 | .054 | .100 | -.026 | .486 |
| | 6 | .187 | .057 | .452 | -.084 | .457 |
| | 7 | .128 | .070 | 1.000 | -.200 | .455 |
| | 8 | .129 | .037 | .325 | -.047 | .304 |
| | 9 | .018 | .037 | 1.000 | -.156 | .192 |

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table 12 – Pairwise comparisons for the Friedman test for lids and proportion of covered rewards accessed in Experiment 2.

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 1 | .850 | 1.354 | .628 | .530 | 1.000 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 2 | 1.000 | 1.354 | .739 | .460 | 1.000 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 5 | -1.450 | 1.354 | -1.071 | .284 | 1.000 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 8 | -1.900 | 1.354 | -1.403 | .161 | 1.000 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 4 | -2.550 | 1.354 | -1.883 | .060 | 1.000 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 6 | -3.100 | 1.354 | -2.290 | .022 | .992 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 7 | -4.050 | 1.354 | -2.991 | .003 | .125 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 10 | -4.450 | 1.354 | -3.287 | .001 | .046 |
| Proportion of Opaque Lids Choice 3-Proportion of Opaque Lids Choice 9 | -4.650 | 1.354 | -3.434 | .001 | .027 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 2 | -.150 | 1.354 | -.111 | .912 | 1.000 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 5 | -.600 | 1.354 | -.443 | .658 | 1.000 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 8 | -1.050 | 1.354 | -.775 | .438 | 1.000 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 4 | -1.700 | 1.354 | -1.256 | .209 | 1.000 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 6 | -2.250 | 1.354 | -1.662 | .097 | 1.000 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 7 | -3.200 | 1.354 | -2.363 | .018 | .815 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 10 | -3.600 | 1.354 | -2.659 | .008 | .353 |
| Proportion of Opaque Lids Choice 1-Proportion of Opaque Lids Choice 9 | -3.800 | 1.354 | -2.806 | .005 | .225 |
| Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 5 | -.450 | 1.354 | -.332 | .740 | 1.000 |
| Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 8 | -.900 | 1.354 | -.665 | .506 | 1.000 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 8** | -.900 | 1.354 | -.665 | .506 | 1.000 |
| **Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 4** | -1.550 | 1.354 | -1.145 | .252 | 1.000 |
| **Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 6** | -2.100 | 1.354 | -1.551 | .121 | 1.000 |
| **Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 7** | -3.050 | 1.354 | -2.253 | .024 | 1.000 |
| **Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 10** | -3.450 | 1.354 | -2.548 | .011 | .488 |
| **Proportion of Opaque Lids Choice 2-Proportion of Opaque Lids Choice 9** | -3.650 | 1.354 | -2.696 | .007 | .316 |
| **Proportion of Opaque Lids Choice 5-Proportion of Opaque Lids Choice 8** | -.450 | 1.354 | -.332 | .740 | 1.000 |
| **Proportion of Opaque Lids Choice 5-Proportion of Opaque Lids Choice 4** | 1.100 | 1.354 | .812 | .417 | 1.000 |
| **Proportion of Opaque Lids Choice 5-Proportion of Opaque Lids Choice 6** | -1.650 | 1.354 | -1.219 | .223 | 1.000 |
| **Proportion of Opaque Lids Choice 5-Proportion of Opaque Lids Choice 7** | -2.600 | 1.354 | -1.920 | .055 | 1.000 |
| **Proportion of Opaque Lids Choice 5-Proportion of Opaque Lids Choice 10** | -3.000 | 1.354 | -2.216 | .027 | 1.000 |
| **Proportion of Opaque Lids Choice 5-Proportion of Opaque Lids Choice 9** | -3.200 | 1.354 | -2.363 | .018 | .815 |
| **Proportion of Opaque Lids Choice 8-Proportion of Opaque Lids Choice 4** | .650 | 1.354 | .480 | .631 | 1.000 |
| **Proportion of Opaque Lids Choice 8-Proportion of Opaque Lids Choice 6** | 1.200 | 1.354 | .886 | .375 | 1.000 |
| **Proportion of Opaque Lids Choice 8-Proportion of Opaque Lids Choice 7** | 2.150 | 1.354 | 1.588 | .112 | 1.000 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion of Opaque Lids Choice 8-Proportion of Opaque Lids Choice 7** | 2.150 | 1.354 | 1.588 | .112 | 1.000 |
| **Proportion of Opaque Lids Choice 8-Proportion of Opaque Lids Choice 10** | -2.550 | 1.354 | -1.883 | .060 | 1.000 |
| **Proportion of Opaque Lids Choice 8-Proportion of Opaque Lids Choice 9** | -2.750 | 1.354 | -2.031 | .042 | 1.000 |
| **Proportion of Opaque Lids Choice 4-Proportion of Opaque Lids Choice 6** | -.550 | 1.354 | -.406 | .685 | 1.000 |
| **Proportion of Opaque Lids Choice 4-Proportion of Opaque Lids Choice 7** | -1.500 | 1.354 | -1.108 | .268 | 1.000 |
| **Proportion of Opaque Lids Choice 4-Proportion of Opaque Lids Choice 10** | -1.900 | 1.354 | -1.403 | .161 | 1.000 |
| **Proportion of Opaque Lids Choice 4-Proportion of Opaque Lids Choice 9** | -2.100 | 1.354 | -1.551 | .121 | 1.000 |
| **Proportion of Opaque Lids Choice 6-Proportion of Opaque Lids Choice 7** | -.950 | 1.354 | -.702 | .483 | 1.000 |
| **Proportion of Opaque Lids Choice 6-Proportion of Opaque Lids Choice 10** | -1.350 | 1.354 | -.997 | .319 | 1.000 |
| **Proportion of Opaque Lids Choice 6-Proportion of Opaque Lids Choice 9** | -1.550 | 1.354 | -1.145 | .252 | 1.000 |
| **Proportion of Opaque Lids Choice 7-Proportion of Opaque Lids Choice 10** | -.400 | 1.354 | -.295 | .768 | 1.000 |
| **Proportion of Opaque Lids Choice 7-Proportion of Opaque Lids Choice 9** | -.600 | 1.354 | -.443 | .658 | 1.000 |
| **Proportion of Opaque Lids Choice 10-Proportion of Opaque Lids Choice 9** | .200 | 1.354 | .148 | .883 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

Table 13 – Pairwise comparisons for the Friedman test for membrane and proportion of covered rewards accessed in Experiment 2.

Each node shows the sample average rank.

| Sample1-Sample2 | Test Statistic | Std. Error | Std. Test Statistic | Sig. | Adj.Sig. |
|---|---|---|---|---|---|
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 1 | .045 | 1.291 | .035 | .972 | 1.000 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 4 | -.864 | 1.291 | -.669 | .504 | 1.000 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 3 | -1.955 | 1.291 | -1.514 | .130 | 1.000 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 6 | -2.545 | 1.291 | -1.972 | .049 | 1.000 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 5 | -2.909 | 1.291 | -2.253 | .024 | 1.000 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 7 | -3.636 | 1.291 | -2.817 | .005 | .218 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 8 | -5.318 | 1.291 | -4.119 | .000 | .002 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 9 | -5.773 | 1.291 | -4.472 | .000 | .000 |
| Proportion of Opaque Paper Choice 2-Proportion of Opaque Paper Choice 10 | -6.500 | 1.291 | -5.035 | .000 | .000 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 4 | -.818 | 1.291 | -.634 | .526 | 1.000 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 3 | -1.909 | 1.291 | -1.479 | .139 | 1.000 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 6 | -2.500 | 1.291 | -1.936 | .053 | 1.000 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 5 | -2.864 | 1.291 | -2.218 | .027 | 1.000 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 7 | -3.591 | 1.291 | -2.782 | .005 | .243 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 8 | -5.273 | 1.291 | -4.084 | .000 | .002 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 9 | -5.727 | 1.291 | -4.436 | .000 | .000 |
| Proportion of Opaque Paper Choice 1-Proportion of Opaque Paper Choice 10 | -6.455 | 1.291 | -5.000 | .000 | .000 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion of Opaque Paper Choice 4-Proportion of Opaque Paper Choice 3** | 1.091 | 1.291 | .845 | .398 | 1.000 |
| **Proportion of Opaque Paper Choice 4-Proportion of Opaque Paper Choice 6** | -1.682 | 1.291 | -1.303 | .193 | 1.000 |
| **Proportion of Opaque Paper Choice 4-Proportion of Opaque Paper Choice 5** | -2.045 | 1.291 | -1.584 | .113 | 1.000 |
| **Proportion of Opaque Paper Choice 4-Proportion of Opaque Paper Choice 7** | -2.773 | 1.291 | -2.148 | .032 | 1.000 |
| **Proportion of Opaque Paper Choice 4-Proportion of Opaque Paper Choice 8** | -4.455 | 1.291 | -3.450 | .001 | .025 |
| **Proportion of Opaque Paper Choice 4-Proportion of Opaque Paper Choice 9** | -4.909 | 1.291 | -3.803 | .000 | .006 |
| **Proportion of Opaque Paper Choice 4-Proportion of Opaque Paper Choice 10** | -5.636 | 1.291 | -4.366 | .000 | .001 |
| **Proportion of Opaque Paper Choice 3-Proportion of Opaque Paper Choice 6** | -.591 | 1.291 | -.458 | .647 | 1.000 |
| **Proportion of Opaque Paper Choice 3-Proportion of Opaque Paper Choice 5** | -.955 | 1.291 | -.739 | .460 | 1.000 |
| **Proportion of Opaque Paper Choice 3-Proportion of Opaque Paper Choice 7** | -1.682 | 1.291 | -1.303 | .193 | 1.000 |
| **Proportion of Opaque Paper Choice 3-Proportion of Opaque Paper Choice 8** | -3.364 | 1.291 | -2.605 | .009 | .413 |
| **Proportion of Opaque Paper Choice 3-Proportion of Opaque Paper Choice 9** | -3.818 | 1.291 | -2.958 | .003 | .140 |
| **Proportion of Opaque Paper Choice 3-Proportion of Opaque Paper Choice 10** | -4.545 | 1.291 | -3.521 | .000 | .019 |

| | | | | | |
|---|---|---|---|---|---|
| **Proportion of Opaque Paper Choice 6-Proportion of Opaque Paper Choice 5** | .364 | 1.291 | .282 | .778 | 1.000 |
| **Proportion of Opaque Paper Choice 6-Proportion of Opaque Paper Choice 7** | -1.091 | 1.291 | -.845 | .398 | 1.000 |
| **Proportion of Opaque Paper Choice 6-Proportion of Opaque Paper Choice 8** | -2.773 | 1.291 | -2.148 | .032 | 1.000 |
| **Proportion of Opaque Paper Choice 6-Proportion of Opaque Paper Choice 9** | -3.227 | 1.291 | -2.500 | .012 | .559 |
| **Proportion of Opaque Paper Choice 6-Proportion of Opaque Paper Choice 10** | -3.955 | 1.291 | -3.063 | .002 | .099 |
| **Proportion of Opaque Paper Choice 5-Proportion of Opaque Paper Choice 7** | -.727 | 1.291 | -.563 | .573 | 1.000 |
| **Proportion of Opaque Paper Choice 5-Proportion of Opaque Paper Choice 8** | -2.409 | 1.291 | -1.866 | .062 | 1.000 |
| **Proportion of Opaque Paper Choice 5-Proportion of Opaque Paper Choice 9** | -2.864 | 1.291 | -2.218 | .027 | 1.000 |
| **Proportion of Opaque Paper Choice 5-Proportion of Opaque Paper Choice 10** | -3.591 | 1.291 | -2.782 | .005 | .243 |
| **Proportion of Opaque Paper Choice 7-Proportion of Opaque Paper Choice 8** | -1.682 | 1.291 | -1.303 | .193 | 1.000 |
| **Proportion of Opaque Paper Choice 7-Proportion of Opaque Paper Choice 9** | -2.136 | 1.291 | -1.655 | .098 | 1.000 |
| **Proportion of Opaque Paper Choice 7-Proportion of Opaque Paper Choice 10** | -2.864 | 1.291 | -2.218 | .027 | 1.000 |
| **Proportion of Opaque Paper Choice 8-Proportion of Opaque Paper Choice 9** | -.455 | 1.291 | -.352 | .725 | 1.000 |
| **Proportion of Opaque Paper Choice 8-Proportion of Opaque Paper Choice 10** | -1.182 | 1.291 | -.915 | .360 | 1.000 |
| **Proportion of Opaque Paper Choice 9-Proportion of Opaque Paper Choice 10** | -.727 | 1.291 | -.563 | .573 | 1.000 |

Each row tests the null hypothesis that the Sample 1 and Sample 2 distributions are the same.
Asymptotic significances (2-sided tests) are displayed. The significance level is .05.
Significance values have been adjusted by the Bonferroni correction for multiple tests.

## Appendix 4. Pilot study on kea physiology

### Introduction

Glucocorticoid hormones (cortisol and corticosterone) are secreted by vertebrate species to overcome stressful situations (Möstl et al., 2009). Corticosterone is the principal glucocorticoid produced by the avian adrenal gland (Möstl et al., 2009). High corticosterone levels have been associated with compromised well-being. Kittiwakes (*Rissa tridactyla*) living in food-poor colonies showed higher levels of corticosterone than food-rich conspecifics (Kittaysky et al., 1999). Similarly, food-restricted hens presented higher levels of plasma corticosterone (Hocking et al., 2001). Parrots that performed feather-damaging behaviour were found to present higher levels of fecal corticosterone (Costa et al., 2016). A pilot study was designed to determine if corticosterone was a well-being indicator for kea.

### Methods

#### Subjects

Three subjects housed at Bristol Zoo Gardens were used for fecal collection protocols: one adult male (Green), one adult female (Purple) and a juvenile female. Table 4.1 presents relevant information about the adults. The juvenile (1-year-old) was the chick of a different pair. She was hand-raised by keepers as the parents were not properly rearing her. The three subjects were housed in the same enclosure, but the juvenile was physically isolated to prevent aggressive interactions. This enclosure was an off-show exhibit. Husbandry was like what is described in Chapter 4.2.

#### Faecal collection protocol

The PI observed kea from a service corridor. As soon as a kea was spotted defecating (easily identifiable as kea raise their tails and walk forwards before defecating), the PI would enter the aviary, collect as much feces as possible with a plastic spoon, introduce the contents into a zip-lock bag and quickly take the sample to a freezer at -20°C. The PI wrote on the bag subject, date, and time. Three samples per week, for three weeks, were obtained for each kea. After all samples were collected, they were sent via mail to Chester Zoo's Endocrine Lab.

#### Corticosterone analysis

Chester Zoo's Endocrine Lab analysed the samples according to their own protocol. Briefly, the pooled sample (made from a portion of each individual sample) was serially diluted alongside their own corticosterone standard. To determine if the assay was able to

measure the hormone, the sample and their corticosterone standard dilutions must show parallelism. No further information was provided.

**Results**

Figure A1 presents the corticosterone binding percentage at different concentrations. Chester Zoo's Endocrine Lab found parallelism between corticosterone and their own marker's binding. Furthermore, statistics were performed with the data Two samples were removed from the analysis as they had to be diluted more than usual.

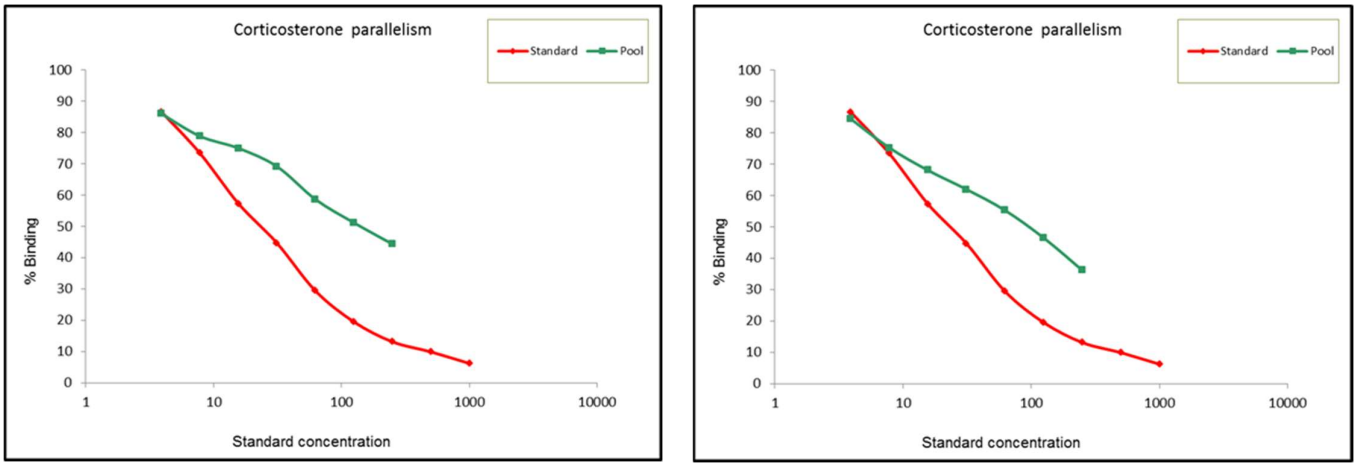


Figure A1 – Left: corticosterone binding percentage for the single male. Right: corticosterone binding percentage for both females.

**Conclusion**

Chester Zoo's Endocrine Lab's results show that there is parallelism between their control and corticosterone from fecal samples. Unfortunately, this only provides information on the presence of corticosterone in kea droppings. It is not possible to make any well-being comments based on these results. Furthermore, glucocorticoid responses are not exclusively associated with negative well-being (Ralph and Tillbrook, 2016). The PI suggests that an experiment is performed (with a larger sample size) to determine the valence of corticosterone regarding well-being (if any) utilizing a biological challenge (if allowed) or providing preferred / non-preferred stimuli and comparing corticosterone levels with a baseline sample.

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